TECHNICAL BULLETIN No. 52 JULY, 1928

A CLASSIFICATION OF THE HIGHER GROUPS AND GENERA OF THE COCCID FAMILY MARGARODIDAE

BY

HAROLD MORRISON

Entomologist, Division of Taxonomy, Bureau of Entomology

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CONTENTS

	Page
Prefatory	1
Introduction	4
Historical	5
General geographic distribution	6
Host relationships	6
Economic importance	7
Relation to other coccids	7
Characteristics considered in developing a classification	10
Habit characteristics	10
Comparative morphology	13
Adult female	13
Intermediate female	22
Larva	23
Adult male	25
Classification	30
Family Margarodidae Morrison	30
Subfamily Xylococcinae Pergande	35
Tribe Stigmacoccini Morrison	37
Tribe Xylococcini Cockerell	40
Tribe Matsucoccini Morrison	48
Subfamily Steingeliinae Morrison	53
Tribe Steingeliini Morrison	54
Classification—Continued.	
Family Margarodidae—Continued.	
Subfamily Margarodinae Cockerell	61
Tribe Kuwaniini Handlirsch	63
Tribe Margarodini Cockerell	71
Tribe Callipappini Handlirsch	82
Subfamily Coelostomidiinae Morrison	86
Tribe Platycoelostomini Morrison	88
Tribe Marchalinini Morrison	91
Tribe Coelostomidiini Morrison	94
Subfamily Monophlebinae Maskell	117
Tribe Monophlebini Cockerell	121
Tribe Drosichini Morrison	158
Tribe Monophlebulini Morrison	173
Tribe Llaveiini Morrison	179
Tribe Iceryini Cockerell	195
List of generic names assigned to the family	218
List of specific names assigned to the family	221
Literature cited	228
Index	237

PREFATORY

As with any other work at all comparable in scope and character, the author is indebted to so many individuals for so great a variety of assistance, much of it indirect, that a complete acknowledgment of benefits received can hardly be made.

Acknowledgment should first be made to C. L. Marlatt, then associate chief of the Bureau of Entomology, under whose general direction the work was performed. As a specialist on scale insects he had much to do with building up the national collection of this group, and he gave personal encouragement and provided adequate support for the work.

Early workers on coccids in the Bureau of Entomology, notably the late Theodore Pergande, have contributed to the present bulletin, chiefly through the careful preservation of rare and valuable material.

The standards of study set in the work of Riley and Howard (*156*)[1] on the genus Icerya might have been followed up with decided benefit to the classification of the group in the years immediately following the publication of their paper. Gifts of specimens to the bureau and to the United States National Museum, by many coccid specialists—Froggatt, Hempel, Kuwana, Leonardi, Marchal, Maskell, Newstead, and by many other entomologists and in particular by E. E. Green and T. D. A. Cockerell—have gone far toward building up a collection sufficiently comprehensive to permit a beginning on work of the type offered here. The larger individual collections of coccid material accumulated by the Bureau of Entomology through its own activities or by gift, including parts of the early collections of Koebele, in Australia and Mexico, the collections of C. H. T. Townsend, in Mexico and Peru, the extensive collections of George Compere, chiefly from Australia, but representing many widely scattered localities, the specimens obtained by R. S. Woglum, in India, and many other smaller collections, have all contributed toward the preparation of this bulletin.

In recent years, while work on the bulletin has been actively in progress, the writer has become indebted to G. Brittin, G. F. Ferris, W. J. Hall, I. Kuwana, C. P. Lounsbury, F. Maidl, J. G. Myers, P. Vayssière, and above all to E. E. Green, for the loan or gift of indispensable study material. It is difficult to acknowledge adequately the extreme kindness and generosity of Mr. Green in sharing material in his collection and in loaning for study unique and other valuable specimens. Mr. Kuwana supplied some very valuable Japanese specimens, including series showing all stages of certain species for which he had worked out the life histories.

Access to the Maskell collection of coccids, commented on elsewhere (*137, p. 1*), has also been a very important factor in the development of the bulletin.

To a series of assistants engaged on the coccid work of the bureau for many years past, the writer is indebted for most of the numerous microscopic preparations that were an absolute requisite for the anatomical studies detailed here.

To the instructing staff of the Bussey Institution, and to those professors of the biological departments of Harvard University with whom he came into contact during the scholastic year 1924–25, the writer is indebted for the acquisition of a broader viewpoint with regard to scientific work, and particularly with regard to taxonomic work, which has manifested itself in this particular study chiefly through a more nearly adequate recognition of the difficulties to be overcome in developing the classification attempted and in bringing it to a satisfactory consummation.

The drawings included have been prepared, under the writer's direction, by several persons; more than half of the number contributed are the work of Miss A. I. Shoemaker. In addition, many of the drawings have been made by Miss Sara Hoke (Mrs. De Vord), by Miss L. J. Kruger, by Emily Morrison, and by the writer himself. A number of the drawings have been taken from previous publica-

[1] Italic numbers in parentheses refer to "Literature cited," p. 228.

tions by the writer and Emily Morrison and are reemployed in this bulletin with some rearrangement and some additions. It has not proved practicable to provide even approximate uniformity of treatment in the illustrating of comparable subjects by different individuals. It is therefore necessary that anyone who attempts to use these illustrations for comparative purposes should comprehend fully that apparent differences in various drawings of the same structure, such as those implied by differences in shading, or by differing thickness of line, are almost certainly of no particular comparative significance. Still another point should be noted in this connection: The figures prepared especially for this bulletin are designed primarily to exhibit generic characters. On this account it may prove that some of them are not sufficiently precise in minute details to serve as exact illustrations of structural characters possessed only by the particular species figured, and they should, in consequence, be used with caution for purposes of specific identification, particularly in genera including numerous species.

Most of the photographic illustrations accompanying the paper have been prepared by J. G. Pratt, photographer for the Bureau of Entomology. The few obtained from other sources are credited individually. For reasons elaborated in the following paragraph, much of the material from which these photographs were obtained was unsatisfactory and often very unsatisfactory. The results, in consequence, leave much to be desired.

As will be evident from the detailed discussions of the geographical distribution of the family and its included genera, the known species are, to an appreciable extent, from regions that, from the viewpoint of a worker in the eastern part of the United States, are decidedly out of the way and relatively isolated. In addition, many of the species, as now known, are to be classed as "rare" or "scarce," since often only a single, or, at most, a very few individual specimens have ever been found. The net result of this situation is that many of the statements regarding structure that have been set down in the following pages have been based on very limited material, often on a single specimen, or even a part of one specimen, a condition which almost inevitably leads to a certain percentage of error, regardless of any conscious effort to avoid this. Again, from a detailed examination of the bulletin it will be evident that there exist several important gaps in the series of stages that have been studied, with those in the adult male stage particularly serious. From these two causes, complete lack of material in some cases, or access to inadequate material only in others, it follows with practical certainty that some of the generalizations made in attempting to characterize fully the tribes and subfamilies accepted in this bulletin will require modification as the unknown or poorly represented stages become available for study, and, in addition, as new forms are discovered.

The present study is essentially a study of the type species or of characteristic representatives of genera, although an effort has been made to broaden the diagnoses presented sufficiently to cover species known to be generically associated with any particular genotype, and sufficiently to indicate the approximate probable limits of each genus.

INTRODUCTION

In the following pages an attempt is made to develop a scheme of classification that will adequately express the interrelationships of the elements making up one of the major sections of the group of insects commonly designated as the hemipterous family Coccidae; to provide a usable basis for the proper generic assignment of species found to belong in this section; and to establish, principally on the foundation of comparative morphology, a basis for the recognition of genera and higher groups as well as of species.

The groups under consideration have, in the past, been looked upon as including the most primitive forms to be found among the morphologically very highly specialized insects classed as coccids. This view, from the information now available, appears to be correct. Quantitatively the total number of presumably valid described species and subspecies or varieties included here, prior to the preparation of this bulletin, was 201, out of a total of a little more than 3,000 described and assumably valid coccid species; the total number of genera, accepted as valid, previously assigned to this group was 31. The tendency for most of the last 25 years has been to group these genera into two units which have usually been designated as subfamilies. It has been found necessary in the present study to increase the total number of genera to 42, in part through the characterization of previously undescribed species and genera, and in part through the breaking up of some of the older genera. The modifications that have proved desirable in respect to the higher groups bear little relation to previous classificatory schemes and are shown in the body of this bulletin.

In one respect, at least, the present effort is unique among papers devoted to the classification of the coccids: For the first time an attempt is made to work out a completely coordinated generic and higher-group classification on the basis of stages other than the customary one, the adult female stage. The fullest possible consideration has been given to the structural characters to be found in the adult male, in the newly hatched larva, and, among those genera in which the intermediate female stages digress strongly in their development from the straight-line type, in these stages as well. Consideration of all of these stages has immeasurably increased the difficulties in the way of the working out of a satisfactory arrangement of the genera into higher groups and has brought the writer to some conclusions that seem to demand the special emphasis that is attempted below.

First, in so far as this particular group of coccids is concerned, the adult male stage of any species possesses morphological characteristics that appear to be of marked value in indicating the broader relationships of the genus to which it may belong—a contradiction of the commonly accepted idea regarding the adult male.

A second conclusion, and, in the opinion of the writer, one that can hardly be emphasized too strongly, is much more difficult to state concisely. It will be attempted thus: Each of these different stages of any single species, or of a genus as a whole, shows, through a series of genera, morphological differences that appear to be of significance in indicating generic relationships or differences and that indicate

permissible combinations of the genera into higher groups. But when such combinations are made on the basis of the morphological characters of the separate stages, and are then compared, it will be found that there is a decided lack of complete agreement in all stages in respect to the limits of any one association of genera to form a higher group. The overlapping is so evident that, by jumping from one character to another without restriction to a particular stage, a complete series of interrelationships can be established running through the whole number of genera included in the family, although the extremes might not be suspected of even the slightest relationship.

Two definite results come from this interweaving of the structural characters: It is, in the opinion of the writer, impracticable to construct any sort of phylogenetic chart or any sort of tabulation that will adequately exhibit the present-day genera as derivatives of a single phylogenetic source; and, with the exception of some very intimate associations of genera, here given standing as tribes, the higher groups that have been defined, and particularly the subfamilies, must be accepted not as arbitrarily and firmly established units, but simply as an evidence of the conclusions derived from a study of the material available for examination.

It is the present belief of the writer that this extensive overlapping and intermingling of characters is actually an expression of the stage in phylogenetic development which the group has now attained, rather than an evidence of uncritical examination of the available evidence bearing on classification. This, if the true situation, offers a logical explanation for the serious confusion now existing in the classification of this group of insects, a condition that is unhappily, but quite obviously, only incompletely remedied in this bulletin.

HISTORICAL

The history of modern classification in these insects starts, as in so many other groups, with Linnaeus. The tenth edition of his Systema Naturae (*115*, *p. 456*, *457*) includes descriptions or citations for two species now included here, *Coccus polonicus* and *C. cacti*. No publication bearing on generic classification appeared until over 70 years later, when, in 1829, Guilding (*83*, *p. 115*) established the genus Margarodes. Shortly thereafter, what eventually proved to be another name for the same genus was proposed by Brandt (*4*, *p. 355*) in Porphyrophora, and a new genus, Monophlebus, was erected by Burmeister (*5*, *p. 80*) for another type of insect belonging in the group. Although a few new genera were characterized during the intervening period, no further important developments along the lines of generic classification came until the publication of Signoret's (*158*, *p. 350–392*) relatively extensive work some 40 years later, when a number of new genera were established and were, with some of the older genera, placed in a group designated as the Monophlebites.

The next attempt to organize the species belonging here into definite genera and higher groups came, after another lapse of nearly 25 years during which time a few more genera were added, in the publications of Cockerell (*17*, *p. 273–275*; *23*, *p. 232*, *257*) in the years 1899 to 1902, when he grouped the genera into certain tribes that

were combined into two subfamilies. This arrangement has persisted in essentially the same form up to the present time,[2] although attention has been called to its unsatisfactory character in recent years (*48, p. 88*), and it is perpetuated in the latest generic classification to be published, that of Vayssière (*168, 170*) for one of these subfamilies, the Monophlebinae. Except for this publication and the exhaustive treatment by Green (*65, p. 422–457*) of the Ceylon species belonging here, published studies in recent years bearing on the generic classification of this group have been limited to the descriptions of a few new genera, and, perhaps more important, to the redescription and recharacterization of several of the more remarkable previously described genera.

GENERAL GEOGRAPHICAL DISTRIBUTION

The geographical range of this family of coccids, taken as a whole, is very wide. Definite records exist showing that at least a single included species has been found in every one of the 6 general zoögeographic regions of the earth, and in the 24 major subregions, excepting only the Celebesian subregion of the Oriental region, the Siberian subregion of the Palaearctic region, and the Canadian subregion of the Nearctic region. The existing exclusion from these last two subregions may possibly prove to be an expression of a natural limitation in the distribution, but it would seem practically certain that representatives will be found in Celebes when it is better explored. Beyond such generalizations it is hardly desirable to attempt to indicate the characteristics of the distribution. While it may be proven ultimately that the largest percentage of these insects has a tropical or subtropical natural distribution, present knowledge of the distribution of members of the group bears a closer relation to collecting or study centers than to direct geographical influences.

The more detailed distribution of the various higher groups and the general distribution of the species included in each genus are indicated in the discussion of each of these.

HOST RELATIONSHIPS

Present knowledge of the actual host relationships of these insects is too fragmentary to justify attempts at generalization. In a few instances, for example with the genus Monophlebulus, there seems to be a rather definite correlation of generic association of the coccid species and of generic or at least of tribal association of the plant hosts, in this case with the host genera Eucalyptus and Melaleuca. This also appears to be true of the genus Matsucoccus, known to occur only on species of Pinus. At the opposite extreme stands Icerya, one species of which, the cottony cushion scale, *I. purchasi* Mask., has

[2] It has proved necessary to ignore completely the classification offered for this group of insects by MacGillivray (*119, p. 45–46, 52–98*). In so far as it relates to these coccids this work is very obviously based so completely on an examination of literature, and, too often, on so careless an examination, that the final product resulting is largely a combination of two sets of errors, and so is of such a nature that it simply can not be discussed concisely with reference to the actual facts of anatomy and relationship. The generic and other group names proposed in MacGillivray's work have, of course, been given the nomenclatorial consideration to which they are entitled from the fact of their having been published.

been recorded by Merrill (*131*) from more than 200 different host plants. As a generalization to which there are many individual exceptions, the tendency among the species treated first, that is, among those insects formerly placed in the subfamily Margarodinae, seems to be in the direction of restriction of the coccid species to one or at most to a few related hosts for each species, whereas the tendency among the species regarded as forming the subfamily Monophlebinae appears to be more toward a less restricted feeding habit.

ECONOMIC IMPORTANCE

At one time certain of the included species possessed an appreciable value as forms whose bodies were useful to man in industry or for medicine (*1*). At the present time the economic importance of the group lies wholly in the injuries which its members inflict on economic plants. One species, the cottony cushion scale, *Icerya purchasi* Mask., has attained a tremendous notoriety as a pest since it began its career in California about 1870, and an equal fame as the subject of an almost classical demonstration of the practicability of the control of insect pests by their natural insect enemies. Its career also supplies an excellent illustration of the serious result of indifference toward the introduction into and the establishment in new localities of actually or potentially injurious insects, as it has gradually spread to many localities throughout the world and has frequently compelled the initiation of extensive campaigns for the introduction and acclimatization of the particular species of predacious beetle that has proved to be its most persistent enemy.

Species of reported economic importance have been noted in genera other than Icerya. Some Margarodes in South Africa and South America attack the roots of grapevines; Xylococcus in the Great Lakes region of North America has caused serious damage to the bark of the canoe birch; one of the species of Matsucoccus, forming gall-like pits in pine twigs, causes appreciable damage to some ornamental plantings; a number of species of Drosicha have been reported as injuring a variety of economic plants in the eastern Asiatic region, from India to Japan, and so on.

The status of the family as a potential source of plant pests has been conclusively exhibited in the experience with the cottony cushion scale. It seems a most obvious conclusion that further dissemination of any of the included species should be absolutely prevented, so far as this is possible.

RELATION TO OTHER COCCIDS

The group of genera considered in this bulletin, and another, usually designated as a subfamily under the name Ortheziinae, unquestionably are more closely related to each other than to any other known coccids. The two groups agree in several particulars, and differ from the remaining groups of coccids in these same particulars. Thus, with at most very rare exceptions, presumably due to an unusual degree of specialization, they both exhibit a varying number of abdominal spiracles in all stages, though these may, under some

conditions and in some species, be very difficult to locate,[3] and, in the adult male stage, they possess well developed compound eyes, except in two known genera. The above possibly indicate all of the absolute characters that isolate these two groups of genera, although detailed knowledge of the actual morphological structures present or wanting in other groups is so incomplete, particularly in the immature and in the adult male stages, that an attempt to give further evidence on specific points is impractical. As generalizations, to which there are many specific exceptions, it may be stated that the groups include moderate to very large species; that certain types of reproductive habit (for example, the development of an internal marsupium [4] or the formation of a definitely shaped ovisac from a band of pores often accompanied by spines or hairs, located on the ventral face of the abdomen) are found only in certain genera placed here; that the adult female frequently has 10 or 11 antennal segments, a number approached, so far as the writer is aware, only in the genus Phenacoleachia, whose single species, *zealandica* is at present regarded as a representative of a distinct subfamily, but whose precise status must apparently remain uncertain until ample study material of all stages is made available; that the adult female frequently has a density of dermal vestiture, consisting of spines, setae, and hairs, not approached by the species of any other group; and that the multilocular disk derm pores in the same stage show a variety of form, of extent of chitinization, and of detail in internal arrangement not exhibited in any other group of genera. Doubtless further generalizations of comparable character can be made when the other groups of coccids have become better known.

In the matter of relationships even less may be said. The obviously closest relatives among the other coccids are to be found in the group of genera currently designated as the subfamily Pseudococcinae; beyond this it is not possible to venture with any approximation of precision.

Following the fashion recently set by Ferris (*6, p. 163; 7, p. 32; 163, p. 432; 53, p. 163*) and Cockerell (*35, p. 47*), the insects here treated have been regarded as forming a family, the Margarodidae. This rank, as now assigned, is not to be considered as an expression of critical opinion except in comparison with the families that have already been established. The elevation of this group of genera to family rank necessitates the establishment of a family for the subfamily Ortheziinae as previously accepted. Orthezia and related genera, while obviously forming a compact and relatively homogeneous group of genera that, from our present knowledge, can not be legitimately broken up into subfamilies, equally obviously are so sharply separated from the groups of genera considered in the present study that assignment to family rank is the only proper method of expressing the relationship existing between the two groups of genera.

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[3] The propriety of this segregation of the coccids possessing abdominal spiracles from all others seems to have been first suggested by Handlirsch (*88, p. 505*) in 1899, but on the basis of very incomplete and inaccurate information.

[4] The condition in *Physokermes piceae* (Schr.) (given as *abietis* Geoffroy), as described by Newstead (*144, p. 132*) in the Monograph of the Coccidae of the British Isles, is not regarded as homologous to or comparable with that found in some of these coccids.

It may be permissible to point out certain logical conclusions that seem legitimate on the basis of this work on these so-called monophleboid genera and a previous study by the writer (*135*) of the ortheziine genera and species, although it should be definitely understood that there is in this no attempt to establish these conclusions systematically. Indeed, there would seem to be some doubt as to the desirability of the present growing crop of "families" in the face of the tremendous gaps that still exist in the knowledge of the comparative morphology of the coccids, to say nothing of the very limited knowledge of the details of the general biological relationships of the included species. These conclusions are as follows:

If the standards set for genera in these papers be accepted as a satisfactory expression of such systematic units, and if the grouping of the genera into families, without particular regard for the intervening units, the tribes and subfamilies, be accepted as an equally adequate expression of a classificatory system, then, since the two groups of genera here designated as the Margarodidae and the Ortheziidae are, apparently very obviously, distinctly separated from the remaining coccids and by characters that on the basis of our present knowledge appear fundamental, and since they are, through the joint possession of these characters, likewise definitely related to each other, then it follows that the logical ultimate unit for designating the coccids as a whole would have subordinal rather than the superfamily rank proposed by Ferris.[5]

In the key which follows an attempt is made to put into brief tabular form a basis for segregating the insects treated in this bulletin from all other coccids; it is not wholly satisfactory and can not be until fuller information is available.

KEY FOR SEGREGATION OF THE FAMILY MARGARODIDAE

a. Abdominal spiracles present in all stages;[6] adult male usually with compound eyes, these rarely lacking, in which case abdominal spiracles should be observable.

b. Larva and all female stages with a distinctly developed flat anal ring bearing pores and six setae; adult males with simple, nine-segmented antennae, with a rather conspicuous spinelike seta at extreme tip of apical segment; penis sheath of adult male appearing strongly bivalved ..... ORTHEZIIDAE.

bb. None of the stages with a flat anal ring bearing pores and setae; adult male nearly always with simple, 10-segmented antennae, rarely with pectinate antennae or with antennae of more than 10 segments;[7] penis sheath of adult male mostly entire or merely cleft at apex, not appearing distinctly bivalved, at most with short bilobate tip; in this case the compound eyes very incompletely developed.

MARGARODIDAE.

aa. Abdominal spiracles wanting in all stages; eyes in adult male not compound as ordinarily accepted and as with the preceding groups, that is, not with hemispherical or otherwise shaped clusters of facets.

ALL OTHER COCCIDS.

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[5] The writer has been much interested in the fact, discovered after the preparation of this statement, that Handlirsch, in Die fossilen Insekten (*89*) and in Handbuch der Entomologie (*90, p. 1134*) makes evident his belief that the coccids are entitled to subordinal standing in any general scheme of insect classification.

[6] Not fully demonstrated for every stage of every species or even of a representative species of every genus.

[7] One species has been described as having nine-segmented antennae.

CHARACTERISTICS CONSIDERED IN DEVELOPING A CLASSIFICATION

Several factors have been given consideration in the effort to build up a scheme of classification for these insects. The ecological relationships, in the very narrow sense of the relation of the members of a genus to their plant hosts with particular reference to the parts of the plants attacked and to the obvious effects on the host, as through the formation of gall-like pits, and striking adaptations to the general environment, such as that shown by many species of Margarodes, have been considered. Attention has been given to the extent to which the known geographical distribution of the species harmonizes with the groups worked out on a morphological basis. What may be termed the "habit characteristics" of the various genera have been examined somewhat more carefully; these seem to be of definite significance, but they usually express themselves quite as well in terms of morphological modification as in statements of actual habit characteristics. Published information on the life cycle of included species has also been considered in relation to each genus; but such information is, in general, so fragmentary that little significance can be attached to the evidence on life histories at present deducible from literature.

The principal reliance in this work has been on characters derived from a study of the comparative external morphology of several stages of each of the included species, so far as those have been available. The study has demonstrated the existence of a multiplicity of morphological characters, perhaps a greater number than will be found in any other group of coccids, which seem to possess definite but varying values as indicators bearing on generic classification. As the variations found in these structures are indicated only briefly in the various diagnoses, it has seemed best to attempt some description of the structures examined and of the modifications of each. Except for the discussion of habit characteristics, these are taken up separately for each of the stages considered.

HABIT CHARACTERISTICS

The simplest type of habit relationship occurring among these insects is that found in those genera, such as Crypticerya and Walkeriana, in which the insects live on the surface of the host without particular adaptation, and in which there is no particular modification of the body of the adult female in connection with the protection of the eggs or newly hatched young, since the eggs are simply deposited directly beneath the somewhat hollowed-out body of the female. The first step in the direction of complication is found in those genera which maintain the same relation to the host, but which produce a loose mass of cottony secretion at maturity, in which the eggs are deposited. An example of this condition is found in Llaveia. Icerya represents a slight further modification in that a definitely shaped ovisac is formed for the retention of the eggs. In genera such as Drosicha the species retain the loose, fluffy mass of secretion, but tend to descend the host trees and form their secretion and oviposit in trash or loose earth at the bases of these.

On another slightly different line of modification are genera that continue to develop without particular adaptation on the surface of the host, principally on the branches or bark, but that tend to show definite modifications of the body, in relation to the reproductive function, beyond the simple development of a special band of secretory pores such as those producing the ovisac in Icerya. Perhaps the first step in this direction is represented by the genus Hemaspidoproctus, in which there is a band of pores around the margin of the ventral surface of the abdomen as in Icerya and, in addition, a definite invagination of the inclosed area to form a cavity or pocket. Beyond this come the forms with a fully formed internal marsupium having a relatively small ventral opening, including such genera as Steatococcus and Aspidoproctus, in which the opening is roughly circular, Labioproctus in which it is narrow V-shaped, and Pseudaspidoproctus with a U-shaped opening.

In respect to habit relationships, those genera in which the intermediate stages show strong divergence from the normal adult type likewise usually show a different sort of modification in relation to the host during the growth period, although they do not show the modifications in relation to reproduction that are exhibited by the genera already discussed. With the single exception of Callipappus, a peculiar Australian genus which has the abdominal segments beyond the third invaginated into the body of the insect to form a large internal marsupium with posterior—not ventral—opening, all of these insects may be classed as without special modifications of the adult female body bearing directly on the protection of eggs and young, although in one sense, since feeding on the part of the adult female occurs only very rarely, if at all, the whole body may be looked upon as modified solely for the reproductive function. In those forms in which the adult female moves about freely as well as in those that may remain within any protective covering developed by the immature stages, the almost invariable tendency is toward the production of a smaller or larger quantity of secreted substance, usually curled wax threads, for the protection of the eggs. The females when free usually seek for additional protection such as that furnished by crevices in bark or soil, beneath partially loosened flakes of bark, or beneath dead leaves and other débris at the base of the host plant, and often oviposition takes place in such a fashion that the dying or dead body of the female supplies an additional protection over the eggs.

It is in this group that the more striking habit modifications take place during the growth period and in relation to the host plant. The simplest relation maintained between host and coccid is that found in such forms as Stomacoccus, in which the intermediate growth stages develop fully exposed on the leaves of the host. A slight modification of this condition is found in genera, such as Neosteingelia, in which the intermediate stages obtain a certain degree of protection by crowding into cracks and crevices in the host bark. Another slight step in modification is found in one species of Matsucoccus, which lives during the growth period concealed and protected within the heart of individual bundles of the needles of the pine which serves as its host.

The larger proportion of these genera show a modification during the growing stages that represents a single type of adaptation with some variation in its detailed expression. This condition consists essentially in the production, by the intermediate stages, of a protective covering usually termed a test, which tends to take on a globular or spherical form and which is mostly very substantial, either through the development of a wall of unusual thickness or of unusual stiffness. While the major portions of such tests are considered to be secreted matter produced by the insect itself, the exact manner of production seems never to have been explained. In some, for example in Neomargarodes, a considerable quantity of foreign matter is incorporated, in this instance consisting of sand grains. Most of these tests have a distinct large opening at a point corresponding to the position of the anal opening in the inclosed insect, but the peculiar glassy tests of Margarodes, commonly known in the regions where they occur by the name "ground pearls," in their perfect condition seem to possess no such passage, but only very minute openings corresponding in position to the location of various structures on the inclosed insect.

This development of a test is frequently accompanied by a most interesting and curious modification of the inclosed insect. The immature or growing stages usually have the posterior apex of the body, which is applied to the circular opening in the test, densely chitinized over an area around the anal opening larger than the opening in the test. This condition likewise sometimes persists in those adult females which through reduction of the legs are compelled to remain within the test, but more frequently it is a large plate on the anterior apex of the head, rather than the posterior end of the body, that is chitinized in the adult. Although there appear to have been no actual observations on the point, it seems self-evident that the adult female, after the last molt and probably after fertilization, reverses the position of its body so that the chitinized plate on the head serves effectually to block the opening in the test.

Accompanying this condition is another curious adaptation. In these forms the anal ring of the immature and particularly of the preadult stages is large and well developed; in the chitinized derm at the posterior apex of the body of this preadult stage, at a distance from the anal opening sufficient to inclose the posterior pair of abdominal spiracles, is an almost precisely circular "breaking joint"; on the large internal anal tube are small lobes or protuberances, or, in one genus, long tentaclelike fingers, the obvious function of which is to induce a close relation between the anal tube of the just molted adult female and that of the preadult. As a result of this condition the anal tube of the preadult is normally retained within that of the adult, and accompanying it is a circular plate of heavily chitinized derm and the two apical abdominal spiracles, all detached from the posterior end of the preadult.

All of the genera here associated in the tribe Coelostomidiini show, with some variation, the general conditions just described. That exhibited by the genus Mimosicerya is probably the most remarkable of all. In this genus the preadult female takes on an approximately globular form and becomes heavily chitinized, but no test is formed. When this stage becomes mature, the anal region breaks away as

already described, and the much reduced adult female, retained within this preadult skin, thus obtains access to the outer world, and, as with other species, guards itself with a heavily chitinized cephalic plate.

A final type of adaptation to the host during the feeding period takes on two general forms. In one of these the insect causes the formation of little pockets in the soft inner bark of the host trees and maintains a direct contact with the outside only through long, secreted wax tubes, one to an individual, that are protruded through cracks or crevices in the covering bark, and that serve to convey the liquid excrement of the insect to a point where it can not possibly come into contact with its body. Some species of Xylococcus show this sort of relation to the host. Others of this genus, settling in the twig axils of the host and growing with the branch, produce slight swellings, hollow within, that may almost be looked upon as true galls. Ultracoelostoma, which forms a spherical test when it simply attaches itself to a twig, apparently can induce a condition intermediate between these axillary pockets and normal tests when it settles down in the axil between two twigs, as a partial cavity covered over by a secreted material seems to be formed under such conditions.

The last habit modification to be remarked on is that found in the relation of the growth stages of one of the species of Matsucoccus, *M. matsumurae*, to its host. Here, in some as yet unexplained fashion, the insect, which lives on various pines, manages to insinuate itself beneath the outer bark layers of the host twigs, and where it attacks in numbers the diameter of infested branches may be increased to a marked degree as the inclosed insects expand during growth.

COMPARATIVE MORPHOLOGY

The terminology employed in discussing the external anatomy of these insects is, in general, that in current usage among workers on coccids. In some cases words have been given a special significance, and an attempt has been made in the discussion immediately following to indicate the limits of such usage. Coccidological taxonomy has recently suffered from so severe an attack of "terminologitis" (*119, p. 24–39*) that a deliberate effort has been made in this bulletin to avoid the introduction of any new words to characterize structures or the modifications of structures.

ADULT FEMALE

SHAPE AND SIZE OF BODY

The shape of the body of the adult female varies widely, although probably the majority of the species are elliptical in outline, either elongate, normal, or short. At one extreme species may be very elongate, with parallel or nearly parallel sides; at the other the outline, particularly in flattened microscopic mounts, may appear to be almost circular. Some species are distinctly ovoid, usually with the abdominal region enlarged, some are very elongate ovoid. In cross section the body may be nearly uniformly elliptical, but there is a tendency toward an approach to a plane surface beneath, which often becomes concave, and toward greater convexity above; sim-

ilarly, in longitudinal vertical section the outline may be merely very elongate elliptical, but much more often the line representing the under surface is nearly straight while that representing the dorsal is strongly bowed and usually highest in the abdominal region. In a few forms the body is globular in shape, or has the longitudinal axis somewhat the longest, and in these the cross section is almost exactly circular. The actual form may vary materially in relation to the degree of maturity that has been attained.

This last is also true of the size, the known limits of which are from 1.5 to 35 mm. A conspicuous example of variation in size in relation to reproductive maturity is found in *Aspidoproctus maximus*, where a recently molted adult female may be as little as 10 millimeters long and rather flat, while the fully matured form may be as much as 35 millimeters long and decidedly convex. In relation to other coccids, the species included here may be classed as large to very large, since many of the species range from 10 to 25 mm. in length, an average condition approached in no other group of coccids.

DERM

As the morphological studies in this group are based wholly, or almost wholly, on specimens that have been treated with dilute potassium hydroxide solution, the term "derm" as here used actually refers to the cuticle as understood in insect histology; and perhaps chiefly to the chitinous component of the cuticle. There is definite variation in the characteristics of the derm in this family of insects. It may be wholly, and almost always is in part, very thin and delicate and very evidently highly elastic. From this condition various gradations may be found with respect to the extent to which thick colored chitin is deposited at full maturity. The adult female of Xylococculus furnishes an example of derm wholly thin and, as it is termed, membranous; Callipappus is an example of heavy chitinization over the whole of the exposed portions of the body. In this last, as in all genera showing even partial heavy chitinization, this is not solid, but is broken up by thin areas in connection with the pores and spines or setae, and often by large circular to oval areolations, covered by very thin cuticle, with pore, spine, or seta in the center of each. In those forms in which a protective plate is developed, only a portion of the derm, either the posterior or the anterior body apex, is heavily chitinized, the remainder usually being very thin and delicate. Except in cases of this sort, the characteristics of the derm chitinization can not be expressed with much accuracy, since there is in these insects, as in many other coccids, a distinct tendency toward a marked increase in the density of the chitinization at complete maturity. The natural color of the chitinized portions of specimens after treatment with potassium hydroxide is yellow brown or, in the case of unusually heavy chitinization, a much darker, sepia brown.

ANTENNAE

Marked variation occurs in the antennae of the various genera included here. The normal type is elongate, although much shorter than the body, with a number of well-developed, nearly cylindrical segments that are usually largest at the base of the antenna and

gradually become smaller toward its apex. These normal segments mostly have the length greater than the transverse diameter, with the basal one or two the shortest and the apical usually longest. Characteristically, each segment bears one or more setae, sometimes so many that a nearly continuous fringe is formed along the distal margin of the segment. In most of the genera, one to several distinctly stouter setae, often with bluntly rounded tips, may be found on the apical segment or on this and other segments. These are here termed sensory setae, on the assumption that they actually have some sensory function, although no experimental proof of this assumption is known. At or close to the apex of the second segment, on the dorsal face, may usually be seen a small, generally oval, double-walled pore, here termed the sensory pore or, when in numbers, as is occasionally the case, the sensory pores. Again no experimental evidence is known to confirm this terminology. This pore (or pores), although not positively located in every specimen examined, is probably present in every species which has antennae that are more than flat plates.

The variations from normal type include complete reduction to the point where there remains only a flat plate, chitinized, set off from the rest of the derm, and bearing one or more setae, as shown by Cryptokermes and Mimosicerya; reduction to nearly cylindrical unsegmented tubercles, as in Xylococcus; reduction to stout cones, rounded at tip, but exhibiting segmentation, as with Ultracoelostoma; or simple reduction in number of segments and in length, as in Neomargarodes. The range of segmentation in the normal type may be taken as from 7 to 11 segments. With all the possible reduction just indicated, the persistence of the sensory setae and pores is noteworthy, although it is not certain that they are always retained.

EYES

The eyes in these insects are reduced to small circular spots, surrounded by more or less chitinization. The variations in the extent of this chitinization are so small and there is so little tendency toward the formation of a basal cone, as in the Ortheziidae, that no variations of apparent significance have been obtained from the eyes, and they are not considered further.

LEGS

In no single species included here are the legs wholly lacking in the stage under discussion. Under normal conditions they are well developed and often large, but definitely shorter than the body, with each of the parts well developed. The coxa and trochanter are very roughly triangular in general outline, and each bears a few to numerous setae. Often the trochanter bears a single distinctly longer seta on its lower edge; this part also bears, on each of the flattened faces, two to several simple sensory pores, resembling those on the second antennal segments. In some genera as many as 16 of these may be present on each face; and in some the trochanter is much elongated and more or less constricted and wrinkled near the middle, hinting at a possible former segmented condition. The femora are almost constant in general shape, elongate, more or less

uniformly swollen, appearing stout or slender in relation to this. The setae borne on the upper portion are almost invariably slender; those on the lower portion may be slender, but are often very stout, resembling heavy spines, or are intermediate in condition. The tibiae are longer than the femora, are usually somewhat enlarged apically, have spines slender above and slender or stout below in general accord with the condition in the femora, but show a strong tendency toward the arrangement of the spines in definite longitudinal rows, particularly those on the under face. Rarely, as in Kuwania, the apex of the tibia bears setae with capitate or knobbed apices, closely resembling this type of claw digitule. The tarsi are large, usually approaching the tibiae in diameter, and are, with a few exceptions, of which Xylococcus is an excellent example, distinctly one-segmented, with setae arranged and varying in size about as in the tibiae, although usually less numerous. In Xylococcus, Stigmacoccus, and Matsucoccus there is a definite division near the base, giving a two-segmented tarsus, although the joint does not appear to be at all flexible. The tarsi do not appear to bear at their apices any setae that may be regarded as definitely homologous with the tarsal digitules of some of the other groups. In no case is there more than a single claw at the apex of the tarsus, and this is entire, more or less strongly swollen at base, and more or less curved and tapering to the tip. There may be a single sharp little tooth or denticle near the tip of the claw, or, sometimes, a series of these, but more often than not no traces of denticles may be seen. Claw digitules arising near the base of the claw are normally present. They may extend beyond the tip of the claw, in which case they are invariably knobbed at apices, or they may distinctly fail to approach or to attain the claw tip, in which case they are tapering and either blunted or acute at tips. They are often delicate, and under such conditions frequently show injury in mounted preparations. Usually one digitule arises from each side of the base of the claw, but sometimes there may be more, up to as many as 12.

The greatest reduction in leg development is found in the genus Xylococcus, where the legs are nothing more than small folds or chitinized globules, without traces of segregated parts. The genus Ultracoelostoma is somewhat less reduced in respect to leg development, as the legs are represented in it by short stout cones, with more or less definite indications of segmentation and with a claw developed. In some other genera, Cryptokermes for example, the legs are perhaps half developed. In most of the remaining genera they are well developed, long, and usually functional. Mimosicerya is an exception to this, as the legs in its adult female stage, while long and showing some evidences of segmentation, are more like everted slender bags or tubes than like functional legs.

BEAK

The beak, often designated in coccid literature as the rostrum, and presumably actually homologous with the labium of insects with normal biting-type mouth parts, is conical in shape in all coccids. In the particular group here considered the cone may be very short and stout, with bluntly rounded tip, or may be rather long, tapering gradually and with slender acute tip. The number

of segments to be observed parallels the length very closely, ranging from one in the short conical beak through two in the moderately conical to distinctly three in the long conical. When the latter condition maintains, the basal segment is always rather narrow, and it often appears only as a very slender ring. While the segmentation has been indicated in each genus in which the beak is present, it should be noted that the distinctness of the joints between the segments is often so debatable that differences of interpretation may very easily arise. Thus, at times, the narrow basal joint appears as hardly more than a thickened rim on the proximal edge of what would normally be the intermediate segment. Again, the joint between the normally intermediate and apical segments sometimes shows itself only as a constriction running around the beak and notching the edges of the labial groove where it meets this on each side; each segment bears some setae, short or long, according to the genus, and the tip of the beak bears a few to many (perhaps 16), definitely differentiated setae that, while most frequently acute at tips, are often bluntly rounded or somewhat expanded and truncate or, in Icerya and its relatives, expanded and slightly notched, almost bifid.

The most conspicuous modification of the beak condition is the fundamental one of presence or absence. Particular emphasis was at one time laid on this point and it was used as a primary basis for separating the two subfamilies in which these insects were then grouped. In recent years it has been discovered that there is marked variation in this matter even within a single species (*51, p. 109*), and that in some genera in which the structure was supposed to be lacking it may actually be wanting or may be represented by irregular folds or thickenings in the derm or may be fully developed, although usually short conical and one-segmented in this event. Along with variability in the extent of beak development goes a comparable variation in the presence or absence or extent of development of the chitinous internal framework of the mouth parts, and the setae or filaments forming the sucking tube. No observations appear to have been made on the problem of the extent to which such mouth parts may be or are used by the insect, and functionally, if not structurally, the dividing line formerly drawn may be a correct one. All of the insects here assigned to the first four subfamilies indicated either have the beak wanting or have a pronounced tendency in the direction of structural and probably of functional reduction. All of the insects assigned to the last subfamily, the Monophlebinae, are supposed to have the beak and mouth parts fully developed and functional, and perhaps all do. The matter is left in doubt, because, in one genus, Protortonia, placed here, the very unsatisfactory adult female specimens available for examination appear to exhibit in these structures a condition of incomplete development, with probable loss of function, comparable to that described as habitual in the other subfamilies.

THORACIC SPIRACLES

Two pairs of thoracic spiracles are present in these, as in all other coccids. These are located ventrally, one just behind each anterior

and each median coxa, although there is some variation with respect to their position between the margin and the middle line of the body. The histology and the internal anatomy of these and of the abdominal spiracles of a fairly typical species have been discussed at some length by Savage (*157, p. 45*), and the present comment is confined to those modifications of details of structure that seem to have taxonomic significance. The opening through the derm, which is surrounded by a chitinized rim, may be almost precisely circular or may be elongate. The derm just outside and distad of this opening may have a definite and sometimes a conspicuous cluster of multilocular disk pores in it, although these are often lacking, more particularly in the smaller species. The cavity just within the opening, termed the atrium by Green (*78, p. 338*), although usually without pores, often has a collar or band or a nearly circular plate, composed usually of multilocular disk pores, around it or at its inner end. Extending inward from the rim surrounding the opening is, in most of the genera, a chitinized plate, broad or narrow, often somewhat expanded at inner end, this the muscle plate of Savage, here simply termed the "bar" of the spiracle. In a few genera, for example in Callipappus, this plate or bar seems to be wholly lacking; in some others it is only poorly developed.

ABDOMINAL SPIRACLES

The abdominal spiracles, which have been demonstrated to be present for all the adult females examined, exhibit variations in number, in position, and in extent of modification that seem to be of marked generic significance. Structurally the abdominal spiracles are relatively simple, consisting of a circular opening through the derm, a cylindrical or somewhat expanded and often bell-shaped chamber or atrium, usually a closing device at the constricted inner end of this apparently consisting of a ring of conical movable hairs, and a short or long narrow tube, without taenidium, leading to the true trachea. The taxonomically important modification of structure relates to the presence or absence of a collar or band of disk pores within the opening and so inside the atrium. Abdominal spiracles when without these pores are here designated as "simple," when with them as "with pores" or sometimes as "complex." The simple type is exhibited by many genera; for example, Icerya and its relatives. The complex type, or type with pores, is exemplified by Perissopneumon among the Monophlebinae and by a majority of the genera in the other subfamilies.

Numerically these spiracles show some interesting variations; the maximum number present is the maximum for any insect—that is, eight pairs—the minimum is two pairs; every intermediate number of pairs is known to occur excepting only five, with seven the number most often present. Even five pairs were reported years ago by the describer (*5, p. 81*) of the type of the genus Palaeococcus, but the latest description of this species, that of Vayssière (*170, p. 267*), credits it with having seven pairs. In a majority of the genera, those with seven pairs present, the missing pair is the anterior one, as shown, for example, by Perissopneumon, Aspidoproctus, and Drosicha. In Icerya and its relatives the reduction has progressed to the point where only the two to four posterior pairs

remain. In another series of forms, represented by such genera as Kuwania and Stomacoccus, the posterior pairs are dropped out, leaving only the four to six anterior pairs. Usually when the posterior pair is present its two members are well separated from the anal opening, but in at least one group of genera, forming the tribe Coelostomidiini, this pair approaches very closely to the anal opening.

As a generalization, the position of the abdominal spiracles may be designated as marginal. Usually, too, the series on each side of the abdomen forms an approximately regular line. Variation and even marked variation may occur in both these points. In Aspidoproctus, for example, the spiracles are well up on the dorsal surface, at least in the undistended early adult females, and in Margarodes the anterior pair of spiracles or sometimes the second pair is far out of alignment with the other pairs and usually much nearer the center of the body.

DERM PORES

As producers of the secreted substance which so frequently conceals or protects these insects, the specially developed pores which are found in the derm play an important part in their lives. Although there is marked specific variation in these pores, apparently they can be segregated into two general types. One of these, found in four genera combined as the subfamily Xylococcinae, has been termed the simple type, since it consists essentially of a thickened marginal rim inclosing a thin, usually slightly granular, surface. Pores of this sort are sometimes not precisely circular in outline, but may be rather asymmetrical, as in Stigmacoccus, where they are numerous. They are, in some cases, faintly divided into segments by indistinct, very narrow lines running from center to margin, with three the usual number of divisions. These pores often resemble very closely small ventral cicatrices.

The other sort present has been termed the multilocular disk type, although at times the number of loculi present is so few as two. In general, this is a flat, circular, platelike pore embedded in the surface of the derm, exhibiting a central area made up of one or a number of loculi and surrounded by a ring of small loculi, this in turn surrounded by a marginal chitinized ring. Many variations occur: There may be several loculi in the central area with these inclosing a small central one; the number of small loculi in the ring varies markedly; the size, shape, extent of chitinization, and the depth of invagination of the central area varies. These pores are described in considerable detail and figured under each genus, so there seems little point to an attempt to describe them more elaborately here. They have proven somewhat disappointing as possible generic characters, and the writer is inclined to believe that their chief use will come in specific differentiation. They have been found in greater or smaller numbers and variety in every adult female examined. In some cases, as in Stomacoccus, only a few are present; in others, as in Aspidoproctus or Drosicha, they are very numerous. Often there is a definite cluster of these disk pores around the genital opening, and they may be clustered or nearly uniformly distributed over other parts of the body. In only a few cases do they appear to be so modified as to have striking taxonomic significance. They are some-

times, in part, much enlarged and deeply invaginated and the presence of a few pores of this type appears to be characteristic of certain genera or groups of genera, as Monophlebulus with large trilocular pores and Walkeriana and its immediate relatives with large bilocular ones.

It seems highly desirable to include a word of caution with reference to the use of these pores for classificatory purposes. When viewed directly from above, any one of these pores that is at all heavily chitinized and that has any appreciable depth varies greatly with respect to the appearance of minute details, as, for example, the shape of the small loculi in the outer band, in relation to the particular point on which the microscope is focussed and in relation to the extent and character of the incident illumination. With changes in these conditions a single pore may furnish half a dozen different pictures of the minute internal details.

DERM VESTITURE

The vestiture or collection of spines, hairs, and setae found on the derm often appears to possess a considerable degree of classificatory significance. As these three terms are each used here in a special sense it seems desirable to attempt to indicate this usage with some accuracy, although it should be recognized in advance that it is by no means certain that the structures designated by these names are homologous throughout the family. There is rather less uncertainty regarding the identity of the setae than of the other two structures. The term seta is here applied to those cuticular appendages which exhibit at the point of attachment a definite chitinized collar, here called the collar or basal collar, the calyx of MacGillivray, in which the seta proper is inserted. These basal collars take on a considerable variety of form; they may be almost cylindrical and rather high or at the other extreme they may be represented merely by a narrow flat ring on the derm. The diameter of this ring is often very much larger than that of the base of the seta proper. Between the two extremes lie varying degrees of height, taper, and size relation between collar and seta. Where the derm is heavily chitinized the setal collar usually appears simply as a thickened rim at the point in the chitinized area from which the seta arises. The typical seta is one with a moderately developed tapering collar that is definitely, but not conspicuously, larger in diameter than the seta itself, while this latter is stoutest at base and tapers uniformly to a slender pointed apex, but with its stiffness and straightness or uniformity of curvature retained throughout. Usually when a seta is broken off the basal collar is retained; when one of the appendages here designated as spines and hairs is detached there remains only a circular, hardly visible hole in the usually almost transparent derm. There is pronounced variation in the stoutness of the setae, this ranging from a condition of extreme slenderness, such as is found in the body setae of some genera, as Stomacoccus and Steingelia, for example, to the very stout, short conical condition found on the legs of many of the larger genera, Llaveia and Aspidoproctus, for example. The setae may be very few in number or they may be very abundant; they may be the only sort of vestiture present, or they may be intermingled with other structures. So far as observations have extended, they are always present in the adult female stage.

The hairs, while suggesting the normal seta in that they are usually slender for much of their length, differ in details of structure. The bases, which are attached directly to the derm without the intervention of a basal collar, are distinctly enlarged, sometimes taking on a hemispherical shape, sometimes a very short conical one, with the slender hair continued from the apex of the hemisphere or cone; often the taper from the enlarged base is only gradual. The extreme tips of these hairs are often very slender and delicate, and appear flexible; in some, however, the tapering portion is rather stout and stiff, and rarely it is rather spinelike in appearance. These particular cuticular appendages may be extremely abundant, as in Drosicha, which may be cited as an example of their optimum development, or they may be very sparse and restricted in distribution, as in Icerya, in which they are probably confined wholly or almost wholly to the ovisac band. They seem to be wholly lacking in a number of genera, for example, in Stomacoccus, Steingelia, Neosteingelia, and others.

The term "spines" is here applied to structures which resemble the hairs in that they lack basal collars, but which are normally much stouter, cylindrical, fingerlike, often somewhat clavate at tips, lanceolate with rather slender tips, and so on. The term has been used also, although with less certainty as to the correctness of the application, for certain actually spinelike, that is, stout conical, acutely pointed structures found in some genera, as Aspidoproctus, Cryptokermes, and Margarodes. The spines, as here defined, are lacking in many genera; when present they may be confined to a few small clusters or may be very abundant and densely crowded, as in Walkeriana. In some genera, at least, they seem to have a function as supports for tufts and plates of secreted matter (in Walkeriana again), and it seems possible, although there is as yet no histological evidence available to support this view, that in these they also function in the actual elaboration of the secretion itself. That this is exuded through a pore at the tip of the spine, as has been suggested for the homologous spines making up the spine bands of Orthezia (*119, p. 106; 116, p. 17*), does not appear at all probable.

ANAL COMPLEX

The anal tube and anal opening, here termed the anal complex, show a marked degree of variation in this group of genera. The opening may be distinctly dorsal in position, although toward the apex of the abdomen, as in the Monophlebinae, or it may be precisely apical, as in species belonging in the Coelostomidiini, or it may be intermediate or subapical in position. Where a distinct tube is developed, the opening itself is not differentiated from the adjacent derm by any sort of thickening or chitinization. The tube may be long and very well developed, with a wide band of polygonal wax pores—pores with an irregular outline and obscurely divided central area —at the inner end, as in Monophlebidus, or it may be apparently wholly lacking along with the anal opening, as in Matsucoccus; various intermediate conditions of size, length, diameter, and presence or absence or extent of development of the polygonal wax pores may obtain. Where the tube is at all developed, there is usually at least a chitinized ring, if not a row of polygonal wax pores, at the inner end; this is not true in some genera, for example, in Marchalina.

If the tube is lacking, there is usually a chitinized ring at the surface, that is, around the opening.

The anal tube is well developed in most of the Monophlebinae, which continue their feeding during the adult stage. In the other subfamilies, in which the mouth parts are doubtfully functional, the anal tube seems to be large, or minute, or wanting in general relation to its development in the preadult stages of each species.

VENTRAL CICATRICES

These structures, the function of which is still unknown, usually appear as clear membranous areas in the ventral derm, each surrounded by a slightly chitinized rim. Under some conditions of preliminary preservation, the inclosed surface may appear very dark and minutely areolate. The number of these that may be present varies tremendously from a single median ventral one, as in some species of Icerya, to several hundred, arranged in transverse segmental rows or bands, not only on the abdomen but also on the thorax and head, and sometimes around the body margins on to the dorsal surface, as in Monophlebulus and Aspidoproctus.

One very interesting fact in relation to these may be mentioned. If the so-called simple pores described in connection with the discussion of the derm pores have in all cases been correctly interpreted, then in the adult female stage ventral cicatrices are to be found only in the subfamily Monophlebinae, while they are completely lacking in this stage of all the other subfamilies, although present in earlier stages in many of the genera.

INTERMEDIATE FEMALE

A general warning notice should be set up with reference to the use of the intermediate female in the development of the present classification. These intermediate stages have been examined critically only in connection with studies on the genera of the first four subfamilies. From the few detailed studies that have been made on the biology of the species grouped here, it is assumed that there are three different stages interposed between the young larva and the adult female in all of these. In most of the genera nothing whatever is known regarding the morphological variations exhibited by these various stages. Much of the material examined in the course of the work has been scant, or very scant. In consequence, it is more probable than otherwise that there has been some confusion of stages in making comparisons and in preparing generic diagnoses. Whether or not any such confusion has been reflected in the present classification remains to be seen.

The range of variation in the different anatomical characters considered in connection with the adult female is approximately duplicated in the preadult and other immature stages, although the variation in any single structure in these stages does not always coincide with that in the same structures in the adult stage of the species. Some differences from the conditions in the adult female may be noted, but there seems to be no prospect of benefit in covering the whole subject again here, since detailed information is available under each genus.

The general situation in the Monophlebinae is for the preadult stage to resemble the adult closely, except for lack of special reproductive devices—an ovisac band, for example—and for a general reduction throughout in size, in number of antennal segments, in numbers of pores and setae, and so on. In a few genera in this subfamily, for example Protortonia and Monophleboides, the preadult is amply provided with cylindrical spines, which are much reduced in numbers or are wholly lacking in the adult.

In the other subfamilies the range of variation in this stage goes beyond that in the adult female in respect to the legs, which are wholly lacking in three subfamilies, the Xylococcinae, Steingeliinae, and Margarodinae; the beak, which is always present, although often small and poorly developed; and the disk pores of the derm, which are sometimes wholly lacking.

LARVA

The larva parallels the adult female with respect to range of variation even more closely than does the intermediate stage in some particulars, although, as it possesses certain distinctive characteristics not found in the adult, it will probably be best to review the structure in this stage briefly.

SHAPE OF BODY

The body outline, as exhibited in microscopic mounts, ranges from short elliptical, as in Xylococcus, to extremely elongate with parallel sides, as in some Margarodes.

DERM

In most genera and species the derm is wholly membranous and usually rather delicate. In Xylococcus the whole posterior apex of the body is chitinized, the area fading out into membranous derm anteriorly. In Ultracoelostoma and Paracoelostoma there is a conspicuously developed, sharply set off chitinized plate around the anal opening.

ANTENNAE

The antennae are usually five-segmented or six-segmented, but have a variation range of from two to seven segments. They are usually stout or moderately stout, but may be slender. They have a single sensory pore at the apex of the second segment. The terminal segment is invariably elongated and is usually enlarged and bears short or long setae, the last sometimes longer than the antenna, and one or more stout sensory setae. These sensory setae sometimes occur on other segments in addition, as on the antepenultimate.

LEGS

The legs, with a single exception, one species of Margarodes, are all present and all fully formed. They vary considerably in relative and actual size and stoutness and have the trochanters with sensory pores and the claw with or without denticle and with varying digitules, as in the adult female leg. The setae on the parts are never heavy and spinelike as in the adult.

BEAK

The structure of the beak in the larva agrees closely with that found in the adult female of the same species.

SPIRACLES

In numbers of pairs and general location, that is, for the abdominal, whether posterior or anterior, the spiracles in this stage agree closely, and perhaps precisely, with the condition in the adult female. They agree fairly closely also in respect to the presence or absence of a bar in the thoracic spiracles, and of internal and adjacent disk pores in both thoracic and abdominal, except that with these single pores usually replace the pore plates or bands or collars of the adult female.

DERM PORES

The same range of types and varieties occurs in the larva as in the adult, but derm pores are often lacking in the larval stage, and when developed are usually less so than in the adult female of the same species; for example, in general they have fewer loculi and are less heavily chitinized and less deeply invaginated.

DERM VESTITURE

Setae are always present and hairs and spines often so, as in the adult female. In certain genera, including most of the tribe Coelostomidiini, additional structures that are perhaps to be regarded as modified spines, but that actually resemble flat buttonlike or mushroomlike disks, may be found toward the posterior apex of the abdomen.

Besides the normal setae found on the dorsal and ventral surfaces of the derm, there is almost invariably present a single pair to three pairs of elongated apical setae, usually much shorter than, but sometimes longer than, the body. There may also be present a series of definite, often long, marginal setae on the abdomen, the thorax, and even on the head.

The spines when present are nearly always arranged in five definite longitudinal bands on the dorsal surface.

The hairs are usually few in number and inconspicuous, but in some genera, for example, Drosicha, they are very numerous, as in the adult.

ANAL COMPLEX

The range of variation in the position of the anal opening and in the possession or lack of definite structures in the anal tube coincides quite well with that described for the adult female.

VENTRAL CICATRICES

Sometimes wanting, usually with a single median, there may be as many as 12 of these present on the abdomen of the larva. Where more than one is present the arrangement may be in a transverse curved line, in a half ellipse, in a median longitudinal row, or in two rows, one on each half of the body. In structure and appearance they resemble the cicatrices of the adult female.

ADULT MALE

As is well known, the adult male coccid differs so strikingly from the adult female that there exists hardly any basis for comparing the two stages. While adult males have been described for many species of coccids—for example, by Green (*65*)—there has been, so far as the writer is aware, no previous attempt definitely to coordinate the structural characters shown by this stage with those found in other stages and to formulate a classification based on the whole. On this account it is hoped that the characters discussed briefly below will be found to provide a basis for placing and organizing the males of some of the other groups of coccids when these are studied comparatively.

Before proceeding to details it may be stated that the normal male coccid of this family is large compared with that of other coccid groups, has an elongate body, no mouth parts, a somewhat expanded and heavily chitinized thorax bearing wings, and a well-developed genital organ, here termed the "penis sheath."

It may be added that all of the characters here considered for the male are microscopic; that is, in this instance, they are characters that have been obtained from microscopic slide preparations, treated with dilute potassium hydroxide, and usually stained. In such preparations characters having to do with shapes and with normal relations of parts are decidedly adversely affected, and they are in consequence very largely ignored here. These preparations likewise prohibit any attempt to study the size, shape, and arrangement of the thoracic sclerites, although it seems possible that a study of these might produce useful information bearing on classification.

SHAPE OF BODY

The males of this family have an elongate body, slender or stout, in general parallel sided, with slight protrusion of the thorax and compound eyes, sometimes with the abdomen somewhat elliptical in shape and so likewise protruding somewhat. The male of a single genus, Stomacoccus, is an exception to the preceding and to nearly every other statement that follows, as it is elliptical, wingless, and without thoracic or head chitinization or compound eyes.

HEAD

As viewed from above, that portion of the head anterior to the compound eyes is usually triangular in outline, with the antennae inserted on the sides of the triangle toward the base. Sometimes the head between the antennal bases is rounded or truncate. The greater portion of the derm of the head is membranous and often bears setae, pores, and true tubercles. There are, however, some chitinized stripes or plates that evidently function as stiffening agents. Usually a median band of this sort runs from the apex of the head down and back along the ventral face of the head and splits to run around the hollow cone into which the oesophagus opens. The mouth is represented only by a tiny simple ring at the inner end of this cone. Other bands may be present and sometimes a considerable portion of the head may be more or less definitely chitinized.

ANTENNAE

The antennae are elongate, often almost linear, sometimes approximating the body itself in length. Very rarely, in the genus Neomargarodes, they are said to be only 7-segmented, with the intermediate segments long-pectinate. All antennae that have been examined in this group have been simple and 10-segmented, although, aside from Neomargarodes, species have been described (in the genus Margarodes) with a range of from 9 to 13 segments. The two basal segments are short, stout, and more or less enlarged; the remaining segments in the simple type are elongate, of approximately uniform diameter, and bear short slender to very long stout setae. Two distinct types of these segments may be found: In one the segment is approximately cylindrical and the setae are not arranged in any definite sequence; in the other the segments are distinctly nodose and have the longer setae arranged in conspicuous whorls. This last type also shows two definite modifications. In one the segments are trinodose, with three whorls of setae, in the other binodose, with two whorls of setae. Any genus of the first four subfamilies, excepting Neomargarodes, will furnish an example of what is here termed the anodose type of segment. Aspidoproctus and Drosicha are two among several exhibiting the trinodose type, while Icerya and its relatives and Monophlebulus show the binodose arrangement.

The relative lengths of the different segments vary. The terminal segment may be shorter than, equal to, or so much as twice as long as the preapical. The apical may be shortest of all, with the third or the fourth the longest, or the third may be shortest.

COMPOUND EYES

With only two exceptions, Stomacoccus, with a single facet, and Steingelia, with a dorso-ventral row of seven facets on each side, the adult males of this group have well-developed compound eyes, usually circular, or at least more or less rounded when viewed from the side, and so roughly hemispherical and semicircular as viewed from above. The facets vary in size and in number. Margarodes and Neomargarodes have the facets larger than do other genera, and also have the eyes strongly elongated dorso-ventrally and approaching or actually meeting below.

OCELLI

In mounted specimens an ocellus usually appears above either the anterior or the posterior angle of the eye. In unmounted specimens its natural position is probably almost directly above the eye. Material is not available for study that will serve as a basis for any general conclusion on this or on the possible taxonomic utility of any relation between the ocellus and the compound eye.

THORAX

With the single exception of wingless Stomacoccus, already mentioned, the thorax in all these genera is somewhat enlarged, rather heavily chitinized, and with definitely formed and outlined sclerites. Only one point has been given consideration with reference to this chitinization: In the males of the subfamilies Monophlebinae and

Coelostomidiinae, so far as known, there is, in the middorsal, that is, presumably, in the mesothoracic region, a transverse, oblong, or elliptical unchitinized area which does not appear in males assigned to the other subfamilies. Doubtless a comparative study of the thoracic sclerites would be profitable taxonomically if sufficient material could be accumulated to permit an attempt at this.

WINGS

In shape, the single pair of developed wings, the mesothoracic, suggests dipterous wings more than those of any other order. While a single general style prevails in these, there is much minor variation with respect to relative length and width, curvature of anterior and posterior margins, relative bluntness and acuteness of tip, and extent of development of anal area. The wings of nearly all monophlebine males are heavily infuscated; those in the other subfamilies are nearly all lightly or very lightly so. Under the microscope each wing shows a minute pattern of varying form, wavy, reticulate, etc., which may prove to have some significance. This pattern is probably most curiously developed in the wing of Matsucoccus, in which it simulates to some degree the venational complexities found in net-veined wings.

The venation is very much reduced and evidently very much specialized. As no material has been available that could be used for studies of the wing tracheae, and as there seems to be a legitimate question as to the correctness of the Patch (*154*) interpretation of the venation, no attempt is made to apply the Comstock-Needham terminology to the veins that can be observed. Superficially examined, most of the wings show a broad, segregated, somewhat thickened band paralleling the costal margin and obliquely truncated well before the apex or gradually narrowed and either approaching or attaining the wing apex, and, arising from some point on the basal half of this, a single well marked diagonal vein that runs toward the posterior margin of the wing, sometimes for only a short distance before fading out, sometimes nearly to the edge of the wing. Occasionally another diagonal vein, usually rather weakly developed, may be seen running from the end of the longitudinal band directly toward the wing apex. There are in addition two folds, appearing as uncolored diagonal lines, one usually arising from the axis of the branching of the longitudinal band and the long diagonal vein, the other arising behind this diagonal vein. The veins just described have in this bulletin been termed the costal complex for the longitudinal band along the anterior margin of the wing, the diagonal or the basal diagonal vein for the longer diagonal vein, and the apical diagonal for the poorly developed, short diagonal occasionally present.

If the veins be examined critically, as in a cross section of the wing, it will be found that the costal complex contains evidence of the presence of two veins, well separated from the costal margin and distinct from each other. The anterior of these is a concave or "low" vein; the posterior a convex or "high" vein. The first diagonal light line represents, in section, the apex of an angle formed by two different planes in the wing and may presumably stand as another low vein. The vein here called the basal diagonal, considered by Miss Patch (*154*) to be the media of the Comstock-Needham sys-

tem, apparently branches from the second or high vein in the costal complex, and is itself a high vein. Immediately following it, and separated from it chiefly by the fact that it forms, in section, the apex of another depressed angle, is another ridge which may be considered as another low vein. Finally the second diagonal clear line may represent still another low vein. If all these indicators be accepted as actually representing veins, and if the theory of alternate high and low veins be accepted in its entirety, then proper interpretation of all these becomes a matter of some complexity. The anterior low vein may quite reasonably be considered to be the subcosta, the high vein immediately following, the radius. The vein here designated as the anterior diagonal, when present, occurs in addition to the first diagonal clear line, and to all appearances is a low vein which must logically, from its origin and appearance, be designated as the radial sector. If, now, the first clear line be regarded as the sector of a vein, it will be the median sector, with the media proper dropped out, a conclusion agreeing with that recently expressed by Lameere (*110*, *p. 131*) in regard to the Homoptera in general. The next two veins or ridges would then represent the cubitus and the cubital sector, which does not wholly accord with Lameere's generalization, since he indicates the loss of the cubitus proper. The second clear line could, on this basis, correspond only to the sector of one of the anal veins, probably the first.

The above is put forward as suggestive only, and, as stated in the early part of the discussion on the wings, the actual terminology employed is very simple and has no relation to any recognized venational system.

By way of an appendix to the preceding, it may be remarked that R. J. Tillyard, after very brief consideration of these wing characteristics, expressed (in conversation) the opinion that the basal diagonal, of this bulletin, represented the cubitus of the Comstock-Needham system rather than the media.

HALTERES

These peculiar organs are well developed in these coccids, excepting only in the wingless Stomacoccus. In some species they are quite broad, almost leaflike, and have one or two short, stout, pointed setae at the apex; in others they are narrower, and sometimes quite slender, with two to several much longer, slender, strongly curved, apically knobbed setae at or near the tip of each; in all cases they appear to hook very firmly into a rather inconspicuous fold or pocket close to the base of the anterior wing.

LEGS

In comparison with the females, the legs of the males are elongate and slender; among themselves varying degrees of stoutness appear, with the maximum in the species of Margarodes, which have the anterior pair still further enlarged and evidently fitted for digging. Species belonging to subfamilies Coelostomidiinae (so far as known) and Monophlebinae have on the tibiae and tarsi and usually on the anterior femora numerous stout, conspicuously bifurcate setae. These have not been found among the males assigned to other subfamilies.

The parts are usually all fully developed and isolated in the legs of these forms, although there may be at least a tendency toward fusion, as in Margarodes. The trochanters have few to many sensory pores on each face. The tarsi are distinctly two-segmented in most of the species, with the basal segment small and triangular. In one genus the joint is very indistinct, and in the subfamily Steingeliinae and the tribe Margarodini the tarsi are distinctly one-segmented. The claw digitules are short or long, acute or knobbed, much as in the adult female; the claw itself is entire, with or without denticle, or, in some species of Margarodes, is conspicuously trifurcate on the middle and hind legs.

ABDOMEN

The abdomen is basically membranous throughout, although frequently transverse, segmental, more or less heavily chitinized plates are present, both dorsally and ventrally, as in Margarodes, to cite a single example. Setae of varying sizes are usually present, and these may become very conspicuous in the Monophlebinae. The species of this subfamily practically always display on the abdomen, and elsewhere, a single type of flat, usually quadrilocular disk pore. These are lacking in some of the other subfamilies. The Monophlebinae also show an abdominal characteristic not found in any of the other groups: At the posterior apex are two long or short but very definite lobes usually termed "fleshy tassels," while the margins of the other posterior abdominal segments sometimes exhibit similar fleshy tassels, so several pairs may be present in some species. There are no traces of these in any of the other subfamilies. Rarely (subfamily Coelostomidiinae, so far as known) there may be transverse bands of small tubular pores on the venter of the segments. In many of the genera, including those in the subfamilies Xylococcinae and Margarodinae, the dorsal preapical segments bear one or two transverse clusters of large, deeply invaginated, tubular pores which, in life, produce a tuft of glassy threads that often exceeds the body in length. The abdominal spiracles are probably always present, although, if so, they are sometimes very difficult to locate. Where they have been checked successfully, they agree in number with those of the female of the species. They are always simple and often very indefinitely developed, appearing as hardly more than slits through the derm.

PENIS SHEATH

At the posterior apex of the abdomen ventrally is a fairly complex organ that is developed in relation to the reproductive function. This structure, which no doubt represents a fusion and modification of the gonapophyses and perhaps other structures in some other insects, is here called the penis sheath. In the form most often observed, it is much broadened and rather high at the inner end or base, while from this a horizontal prong protrudes backward, tapering strongly or gradually, as viewed from above, and terminating in a rounded, or cleft, or sometimes deeply bilobed tip. This is termed the sheath proper. The dorsal face of the basal portion, leading to the interior of the abdomen, is broadly cut away to permit passage of the large and often very long "fleshy" penis which sometimes exceeds the abdomen in length and bears numerous slender spines and often a

patch of very short, flattened, pectinate ones. Beneath and more or less flexibly hinged to the sheath proper is a plate, called here the ventral valve, which is usually thin and flattened, and distinctly shorter than the sheath proper, but which in a few genera is somewhat elongated, slightly curved downward and slightly expanded at tip, as in Neosteingelia, for example, or in other genera is much elongated, slender, and strongly curved downward, decidedly exceeding the apex of the sheath proper, as in Stomacoccus and Steingelia. In this last genus the sheath is very short and has an appearance at the apex as of two separate lobes approaching each other. A definite, simple, rather large anal ring may usually be observed directly above the penis sheath.

CLASSIFICATION

FAMILY MARGARODIDAE MORRISON

This family was established very recently by the writer (*136, p. 99*) for the reception of the subfamilies and genera discussed in the following pages.

FAMILY CHARACTERISTICS

Habit.—Various, living during the growing period on leaves, stems, branches, trunks, or roots of the host, free or concealed beneath bark or in gall-like pits, naked or protected by dense waxy secretion or a firm, usually globular test of secreted material; adult female at maturity depositing eggs beneath body, in a loose mass of cottony secretion, in a definitely formed posterior ovisac, in an internal pouch or marsupium, or within the gall-like pit or the heavy walled test within which it has developed.

Adult female.—Size small to very large; body varying much in outline, elongate, with nearly parallel sides, elongate ovoid, elongate elliptical to stout ovoid or elliptical, nearly circular; derm membranous throughout or more or less heavily chitinized in particular areas or in entirety; antennae varying greatly from a normal 11-segmented type down to small flattened or invaginated plates bearing one or more setae, where at all well developed with one or more sensory pores on the apex of the second segment, and usually with enlarged sensory setae on at least the apical, and often on the other segments; legs more or less developed, varying from long and stout, fully formed, to small conical stubs, with the divisions separating the parts incomplete, almost always with claw formed, more or less curved, with or without denticle, claw digitules nearly always present, short and acute to longer than claw and knobbed at apices, trochanters with two to several sensory pores on each face, setae on parts slender to very stout, spinelike, tarsus usually one-segmented, rarely two-segmented; beak often completely lacking or incompletely developed, where present varying from very short, bluntly conical, to elongate, slender conical, segmentation correlated more or less definitely with the length, with one, two, or three segments, apex of beak bearing a few to many somewhat enlarged sensory setae with tips slender and acute, bluntly rounded, truncate, widened or almost bifid; thoracic spiracles present, in two pairs, each without or, much more frequently, with bar, with or without disk pores on derm just outside the opening, opening elongate to circular; abdominal spiracles always [3] present, the number of pairs varying from eight to two, where less than eight the reduction occurring most frequently from the anterior end, leaving only the posterior pairs, but sometimes from the posterior end, leaving the anterior pairs, with or without disk pores within atrium, and with or without a more or less definite cluster of pores on the derm about the opening of each, posterior pair, when apical, widely separated from anal opening or intimately associated with this, all usually much smaller than thoracic spiracles, sometimes about equal in size, rarely larger; derm pores varying from simple circular or irregular disks to

[3] These are often difficult to locate, and have not as yet been definitely found in every stage of every species examined.

large and deep bilocular or trilocular pores, mostly flat multilocular disk with extensive variation in the size, shape, extent of chitinization, and details of internal arrangement, sometimes entirely wanting, or with very few, or fairly numerous or very numerous; derm bearing setae, these rarely few in number, usually rather numerous, varying much in size, chitinization, shape of basal collar, and so on; usually with hairs, these rarely wanting, often very few, occasionally very numerous and densely crowded; with or without spines, these, when present, cylindrical to conical, slender to stout, few to very numerous, and densely crowded; anal opening apical, subapical, or distinctly dorsal in position, sometimes surrounded by a cluster of pores and hairs or setae, or by all three, opening itself distinctly chitinized only where tube is not formed; anal tube small or large, long or short, without or with a chitinized ring at inner end, without or with polygonal wax pores at inner end; ventral cicatrices completely lacking or more often present, in this case with one to very many (into the hundreds), shape varying, circular, elliptical, very elongate, and so on.

Intermediate female.—Varying greatly, closely resembling adult female or very much modified; body shape elongate elliptical or ovoid to globular, with nearly circular outline; naked, more or less covered with secretion, or concealed within a heavy or delicate secreted test or within gall-like cells beneath the host bark; derm membranous or more or less completely chitinized; antennae varying from fully developed, but usually with fewer segments than in adult, to nothing more than flat or somewhat invaginated plates bearing one or more setae, perhaps very rarely wanting, where fully developed with pores and setae arranged much as in adult; legs likewise varying greatly, fully formed and of normal length, much reduced, conical, flat plates on derm, or wholly wanting, when appreciably developed with claw and digitules, the first with or without denticle or denticles, the second acute and not reaching claw apex, or knobbed and surpassing it, trochanters mostly with only a few (two to four) sensory pores on each face; beak more or less developed, small, short, stout conical to elongate conical, one-segmented to three-segmented, apical sensory setae acute to almost bifid as in adult; thoracic spiracles without or, more frequently, with bar, without or with disk pores or pore plate within atrium, without or with a band or cluster of disk pores on derm at opening; abdominal spiracles as in adult, number of pairs varying from eight to two, larger than, equal to, or much smaller than thoracic, with or without disk pores within atrium, reduction taking place from either the anterior or posterior end of the abdomen; derm pores with much the same types and modifications as in the adult female; derm setae, spines, and hairs often much as in the corresponding adult female, sometimes much reduced in size and numbers even when abundant in the adult female, sometimes wholly or almost wholly wanting; anal opening varying as in adult, sometimes very difficult to locate; anal tube also varying within about the same limits as in adult; ventral cicatrices usually present, rarely lacking, number and arrangement varying within same limits as in adult.

Larva.—Body outline stout elliptical to very elongate, with parallel sides; derm membranous or with the posterior apex chitinized; antennae stout to slender, short to elongate, with short setae or with some setae longer than the body, usually with stouter sensory setae on apical segment, rarely with these on other segments, second segment usually with a single sensory pore, number of segments ranging from two to seven; legs usually normally developed, sometimes with the anterior pair much enlarged and much stouter, very rarely with the posterior two pairs wanting, trochanters usually with two sensory pores on each face, tarsus one-segmented, claw with or without denticle, claw digitules acute and not attaining claw apex or knobbed and surpassing apex of claw; beak always present, short to long conical, one-segmented to three-segmented much as in adult, apical sensory setae acute to bifurcate as with adult; thoracic spiracles with or without bar, with or without disk pores within atrium, with or without disk pores on derm at mouth, the range of variation much the same as with adult; abdominal spiracles in from eight to two pairs, not certainly located in a few forms, size varying from slightly larger than thoracic to minute, hardly visible under high magnification, with or without pores within atrium, reduction from anterior or posterior end of abdomen as with adult; derm pores showing much the same types as in adult, but usually less developed, pores sometimes wholly lacking; derm with or without spines, usually with, sometimes without hairs, and with at least a few setae, these sometimes numerous; apex of abdomen, with very rare exceptions, bearing at least one and often two or three pairs of enlarged, definitely differentiated apical setae, these ranging in size from perhaps one-

tenth to perhaps two or three times the length of the body, and often accompanied by a more or less complete marginal fringe of similar setae on abdomen, or even on head and thorax in addition; anal opening dorsal, subapical or apical, sometimes apparently very much reduced, sometimes surrounded by a circle of small, usually fimbriate hairs, not chitinized itself except where tube is not developed; anal tube, when developed, chitinized or membranous, with or without chitinized ring at inner end, with or without a collar of polygonal wax pores at inner end, with or without disk pores associated; ventral cicatrices rarely lacking, usually with a single median, but with one to several in varying arrangement on the ventral face of the abdomen.

Adult male.—Body elongate, of varying stoutness; head membranous except for chitinized thickened bands, mostly ventrally, very rarely (one genus) wholly membranous; antennae attached between the eyes and the apex of the head, the two basal segments enlarged, the remainder distinctly more slender, rarely with the intermediate segments long pectinate and a total of seven segments present, usually simple, 10-segmented, with the segments beyond the second cylindrical, entire, and with the setae distributed irregularly, or trinodose, with the longer setae in three whorls, or binodose, with the setae in two whorls, range of antennal segmentation reported in various descriptions 9 to 13; compound eyes almost always present, these very rarely reduced to a single facet each, or to a dorso-ventral row of facets on each side of head, eyes usually rather strongly convex and strongly protruding, circular or more or less flattened in outline as viewed from the side, sometimes much drawn out dorso-ventrally, with the lower ends approximated or actually meeting below; ocelli placed above the compound eyes, usually appearing at either the anterior or the posterior corners in mounted specimens; thorax nearly always heavily chitinized (membranous and wings wanting in one genus), the middorsal area entire or exhibiting a conspicuous transverse oblong to elliptical unchitinized area; legs mostly slender to moderately stout, rarely stout with the anterior pair still more enlarged and fitted for digging, trochanters with few (2) to many (around 15) sensory pores on each face, tibiae and anterior femora with or without numerous conspicuous bifurcate setae, tarsi usually two-segmented, sometimes one-segmented, claws with or without denticles, claw digitules usually two in number, sometimes as many as 12, acute and not attaining claw apex, or knobbed and surpassing claw apex; wings rarely lacking (one genus), usually present, nearly clear to strongly infuscated, costal margin bright red or dark in color, costal complex truncate before wing apex or tapering and attaining apex, with a basal diagonal, this long or short, occasionally with an apical diagonal, normally with two diagonal light streaks, these hardly observable in some wings, shape of wing various, usually at least slightly broader toward base and tapering toward apex; halteres narrow to broad leaflike, with one to several setae at or close to apex, these short and stout, pointed, or long, slender, curved, and knobbed at tips; abdomen membranous, with or without transverse segmental chitinized plates, with abdominal spiracles, presumably numbering as in other stages, often obscured and difficult to locate, margin with or without long or short "fleshy tassels," total number, when present, varying from 2 to 12; penis sheath varying much in shape, usually stout at base, tapering more or less to a slender rounded apex, sometimes cleft and bilobed at apex, rarely (one genus) appearing slightly bivalved, lower valve short and truncate at apex to long slender, curved downward and pointed at apex; derm of abdomen with or without flat disk pores with trilocular, quadrilocular, or quinquelocular centers, and with or without one or two transverse oval or elongate clusters of long, deeply invaginated, multilocular, tubular pores, rarely with transverse segmental rows of small tubular ducts on the ventral face of the abdomen.

The genera that are included here have been grouped in five subfamilies. As has been emphasized elsewhere, this arrangement is not based on clear-cut, conspicuous differences appearing consistently in all of the stages studied, since such do not seem to exist, but rather on single or at most a few characteristics appearing in perhaps one stage only of a genus and often only inadequately supported by the other characters studied.

These subfamilies may be more or less satisfactorily separated by the following keys:

KEYS TO SUBFAMILIES OF MARGARODIDAE

ADULT FEMALE

a. Tarsi distinctly two-segmented, except rarely, when leg is reduced to a small protuberance without segmentation; disklike simple pores present. XYLOCOCCINAE

aa. Tarsi one-segmented, legs, if reduced, with some segmentation; disklike simple pores wanting.

b. Claw with several (6 to 12) large knobbed digitules surpassing apex of claw; antennal bases actually contiguous STEINGELIINAE

bb. Claw usually with two digitules, these knobbed and surpassing the claw apex, or short and not attaining claw apex, if with more than two then these short, acute, not at all conspicuous; antennal bases often close together but not actually contiguous.

c. Anal tube, if well developed and with ring at inner end, with opening distinctly apical in position; opening sometimes subapical, the tube in this case poorly developed or wanting; no ventral cicatrices.

d. Usually with disk pores, in a band or plate, within atrium of thoracic spiracles, if without these, then the anterior legs much enlarged, fitted for digging; very rarely with disk pores externally at opening of thoracic spiracles; antennae mostly quite normally developed, very rarely tending to conical form, in this case distinctly and sharply segmented. MARGARODINAE

dd. Without disk pores or pore plate within atrium of each thoracic spiracle, although usually with a cluster or band of these externally at opening of each; antennae rarely fully developed, mostly reduced to short cones retaining linear segmentation, to joints, or to flat plates on derm. COELOSTOMIDIINAE

cc. Anal tube always well, or at least relatively well developed and with a simple ring or a band of pores at inner end, the opening distinctly dorsal in position, although at various distances from the apex of the abdomen; ventral cicatrices present, varying much in number, size, and arrangement MONOPHLEBINAE

INTERMEDIATE FEMALE

a. Legs wholly lacking; antennae reduced to flat plates.

b. Each thoracic spiracle with one to several very tiny setae set in relatively large collars on the derm behind or beyond its opening. MARGARODINAE

bb. Without such tiny setae in association with each thoracic spiracle.

c. With seven or eight pairs of abdominal spiracles; if with seven, these the posterior pairs XYLOCOCCINAE

cc. With six pairs of abdominal spiracles, these the anterior pairs. STEINGELIINAE

aa. Legs present, rarely only as flat differentiated plates on the derm, more often as conical protuberances, but usually fully developed, normal, closely resembling the legs of the adult female; antennae in some genera reduced to stout cones, these retaining distinct evidences of segmentation, or more frequently elongate, normal, with several distinctly separated segments.

d. Antennae and legs usually reduced to short or elongate cones, but with definite evidences of segmentation, rarely elongate, normal in form, the anal opening in this case distinctly apical, the tube either without ring at inner end and abdomen without ventral cicatrices, or, if with ring, the tube breaking away with a circular disk of the surrounding derm at maturity, leaving a large circular opening at posterior apex of body and with ventral cicatrices present COELOSTOMIDIINAE

dd. Antennae and legs fully developed, normal in size and shape; anal opening distinctly dorsal, anal tube with ring, and with or without polygonal wax pores at inner end MONOPHLEBINAE

LARVA

a. Anal opening usually distinctly apical in position; if subapical or apparently dorsal, then the anal tube not developed.
b. Anal tube well developed, with polygonal wax pores at inner end; ventral cicatrices present, arrangement various, always more than one.
c. Ventral cicatrices arranged in a single median ventral row, two to seven; beak short conical, one-segmented, attached opposite the middle coxae---------- XYLOCOCCINAE (part only)
cc. Ventral cicatrices not in a single median ventral row, either in a transverse row or in two intermediate rows, one on each half of the venter of the abdomen; beak long conical, three-segmented, attached opposite anterior coxae-- COELOSTOMIDIINAE (part only)
bb. Anal tube poorly or not at all developed, rarely with ring, and in no case with polygonal wax pores at inner end; ventral cicatrices wanting or only a single median one present.
d. Antennae normally seven-segmented---------- COELOSTOMIDIINAE (part only)
dd. Antennae normally six-segmented, rarely five-segmented.
e. Body with numerous setae, the apical pair not definitely differentiated; anal tube chitinized, but without ring at inner end; no ventral cicatrix---------- COELOSTOMIDIINAE (part only)
ee. Body setae not numerous, one or more apical pairs distinctly differentiated; anal tube usually not developed, sometimes as in preceding; cicatrix present or wanting.
f. With a single, median, circular, ventral cicatrix, this often small---------- MARGARODINAE (part only)
ff. No ventral cicatrix.
g. Claw digitules lacking; second and third antennal segments with lanceolate setae; with very tiny bilocular derm pores; with a fringe of large marginal setae on abdomen---------- MARGARODINAE (part only)
gg. Claw digitules present, knobbed and surpassing claw apex; no lanceolate setae on antennae; no large marginal abdominal setae.
h. Antennae with enlarged, stout, sensory setae on at least one preapical segment; with the seven posterior pairs of abdominal spiracles developed---------- XYLOCOCCINAE (part only)
hh. Antennae without enlarged sensory setae on preapical segments; with the four to six anterior pairs of abdominal spiracles developed.
i. Claw with a distinct denticle. MARGARODINAE (part only)
ii. Claw without denticle---------- STEINGELIINAE
aa. Anal opening distinctly dorsal in position, sometimes fairly close to apex of abdomen, anal tube well developed, with at least a chitinized ring at inner end and nearly always with polygonal wax pores there. MONOPHLEBINAE

ADULT MALE

a. Legs (tibiae, tarsi, and anterior femora) bearing bifurcate setae; mid-dorsal area of thorax with a conspicuous, transverse, elliptical to oblong, unchitinized area; without clusters of long tubular pores dorsally near apex of abdomen.
b. Apex and lateral margins of abdomen with at least one and frequently with several pairs of "fleshy tassels," these short or long but always distinctly developed---------- MONOPHLEBINAE
bb. Apex and lateral margins of abdomen with no suggestion of the development of fleshy tassels---------- COELOSTOMIDIINAE
aa. Legs without bifurcate setae; mid-dorsal area of thorax without a transverse unchitinized area; with one or two clusters of long tubular pores near apex of abdomen dorsally, these very rarely wanting, the compound eyes, and sometimes the wings and thoracic chitinization also, lacking in this case.

c. Compound eyes reduced to a row of facets on each side of head or to a single facet; wings, halteres, and thoracic chitinization sometimes lacking; tarsi distinctly one-segmented, digitules knobbed and slightly exceeding claw apex ---------- STEINGELIINAE

cc. Compound eyes well developed, with numerous clustered facets; wings and halteres always present; tarsi usually plainly two-segmented, rarely indistinctly so, and rarely definitely one-segmented, if the last, then the anterior legs much enlarged, heavily chitinized, fitted for digging; digitules usually acute and not attaining claw apex, rarely knobbed and exceeding it.

d. Halteres mostly broad and flat, each usually with one, rarely with two, short, stout, acute, at most only slight curved setae at or close to tip---------- MARGARODINAE

dd. Halteres mostly narrow, with several (four to six) long, slender, curved, distinctly knobbed setae at or close to apex. XYLOCOCCINAE

SUBFAMILY XYLOCOCCINAE PERGANDE

This subfamily was erected by Pergande (*100, p. 26*) in 1898 for the reception of the genera Xylococcus and Coelostoma (=Coelostomidia). In subsequent literature the included genera were placed in the subfamily Margarodinae and Pergande's subfamily name was abandoned until reemployed by MacGillivray (*119, p. 80*). The limits of the subfamily as treated here are very different from those indicated by both of these writers.

SUBFAMILY CHARACTERISTICS

Habit.—Living during the growth period under various conditions, exposed freely on the host, protected within the bundles of needlelike leaves, concealed beneath and protected by the bark of the host, forming gall-like pits or cavities beneath the host bark or in the host twig axils, or forming a heavy globular test.

Adult female.—Body elliptical or ovoid to rather elongate elliptical, rarely (one genus) with chitinized plate on head or (one genus) with posterior apex more or less chitinized; antennae normally well developed, normally nine-segmented, sometimes with fewer segments, sometimes with sensory setae on apical segments only, sometimes on preapical as well, bases not contiguous, second antennal segment bearing several (three to four) sensory pores, antennae rarely (one genus) reduced to small cylindrical tubercles, without segments, but bearing sensory setae and pores; legs rarely (one genus) reduced to small folds or globular tubercles, usually well developed, without fusion of parts, with the tarsus rather distinctly two-segmented, the basal segment much shorter, this in contrast to the one-segmented tarsi of all the other known members of this family, trochanters with several to many (5 to 14) sensory pores on each face, claw without, or at most with a very faint denticle, claw digitules simple, acute, not attaining tip of claw or rarely (one genus) knobbed and exceeding tip of claw; beak, where present, usually incompletely developed, at most obscurely one-segmented; thoracic spiracles with or without an at least partially developed bar, with or without disk pores on derm at opening of spiracles, mostly smaller than or only slightly larger than the abdominal pairs; abdominal spiracles in seven to eight pairs, these the posterior ones if in seven pairs, with or without pores within atrium; derm pores showing some variation, one type with circular to oval to bilocular to multilocular centers with or without a submarginal band of small loculi and another circular to irregular, simple with apparently finely granular surface, sometimes very vaguely divided into two, three, or four irregular loculi, these last pores in some species much resembling small ventral cicatrices; derm without spines; hairs sometimes certainly, and perhaps always, present in small numbers; setae present, sometimes quite stout, almost spinelike, usually fairly numerous; anal opening apical, either fairly definitely formed, but not conspicuous, or practically undeveloped; ventral cicatrices wanting (see discussion under pores).

Intermediate female.—Body globular to rather elongate elliptical or ovoid, derm membranous to fairly heavily chitinized; antennae reduced to flat plates bearing one or more sensory setae; legs wholly lacking; beak very short conical, poorly developed, one-segmented; thoracic spiracles of moderate size, usually without, rarely (one genus) with bar, with or without disk pores within atrium, with no tiny setae on derm behind opening; abdominal spiracles in seven to eight pairs, these—the posterior ones—if in seven pairs, usually with pores within atrium of each; usually with at least a few disk pores on derm, these rarely lacking; derm rarely (one genus) with spines, these usually lacking; hairs rarely present, usually apparently wanting; setae present, usually in numbers although not tending to be densely crowded; anal tube rarely small and inconspicuous, usually large and very strongly developed, bearing numerous pores, and, in one genus, prominent internal prongs radiating from the inner end; ventral cicatrices wanting.

Larva.—Body elliptical to stout elliptical; posterior apex chitinized, or whole derm membranous; antennae fairly stout to stout, six-segmented, either the apical only, or apical and some preapical, with sensory setae, bases close together, but not contiguous; legs normal, claw with or without denticle, all claw digitules knobbed and exceeding tip of claw; beak attached opposite middle legs, short conical, one-segmented; thoracic spiracles with or without bar, without pores within atrium; abdominal spiracles in seven to eight pairs, these the posterior if in seven pairs, with or without pores within atrium; derm pores present or wanting, if present including multilocular disk type with circular center and bilocular disk type; derm without spines, without small chitinized disks, with or without hairs, with setae, these mostly small and in fair numbers, with a single pair of enlarged, but not conspicuous, apical setae; anal tube apical, very well or poorly developed; ventral cicatrices wanting or present as a single median abdominal row of two to seven.

Adult male.—Of the usual elongated shape; apex of head not acute; antennae simple, slender to moderately stout, segments beyond second approximately equal in length but the apical shortest of these; legs without bifurcate setae, the trochanters with few to many (three to eight) sensory pores on each face, tarsi two-segmented, the joint in one genus (Matsucoccus) very indistinct, the tarsi here in superficial appearance one-segmented; wings narrow, very slightly clouded, basal diagonal short to elongate, costal complex continued to wing apex as a tapering band, or truncate well before wing apex, apical diagonal faintly present or lacking; halteres somewhat expanded, apical setae long, slender, numerous (four to six), apices more or less distinctly knobbed; abdomen with heavily chitinized transverse plates or almost wholly membranous, with one or two transverse clusters of tubular ducts dorsally at posterior apex; disk pores present or wanting; penis sheath stout at base, apex entire, ventral valve equalling or somewhat exceeding tip of sheath, slightly expanded at apex and slightly curved downward.

Three tribes embracing four genera are included here. These, so far as the stages are known, may be separated by the following keys:

KEYS TO TRIBES OF XYLOCOCCINAE

Adult Female

a. Anterior apex of body bearing a heavily chitinized, approximately circular plate; genital opening surrounded by a series of clusters of small disk pores ..... Stigmacoccini

aa. Anterior portion of body not so chitinized; genital opening not surrounded by clusters of disk pores.

b. Thoracic spiracles with or without bar, this usually not strongly developed, and with pores within atrium; abdominal spiracles with pores within atrium; abdominal spiracles definitely larger than thoracic; anal tube usually distinctly developed, quite evident ..... Xylococcini

bb. Thoracic spiracles without bar, without pores within atrium; abdominal spiracles without pores within atrium; abdominal spiracles definitely smaller than thoracic; anal tube very poorly developed, hardly or not at all evident ..... Matsucoccini

INTERMEDIATE FEMALE

a. Thoracic spiracles with bar; derm bearing numerous spines; anal tube large, bearing numerous simple disk pores and several (around seven) long tapering branches at inner end ---------- STIGMACOCCINI

aa. Thoracic spiracles without bar; derm without spines, sometimes with spine-like setae; anal tube often well developed and bearing bands of wax pores, but in any case without simple pores and without long internal branches.

b. Thoracic spiracles without disk pores within atrium; derm bearing some multilocular and some simple disk pores; with eight pairs of abdominal spiracles; anal tube very well developed, bearing bands of wax pores near and at inner end; posterior apex of body heavily chitinized. XYLOCOCCINI

bb. Thoracic spiracles with disk pores within atrium; derm without disk pores; with seven posterior pairs of abdominal spiracles; anal tube very poorly developed, without traces of pores; no differentiation in extent of body chitinization ---------- MATSUCOCCINI

LARVA

(The larva of Stigmacoccus is not known)

a. Posterior apex of body heavily chitinized; with sensory setae on apical antennal segment only; claw without denticle; derm with disk pores; thoracic spiracles with bar ---------- XYLOCOCCINI

aa. Posterior apex of body not heavily chitinized; with sensory setae on an intermediate antennal segment; claw with denticle; derm without disk pores; thoracic spiracles without bar ---------- MATSUCOCCINI

ADULT MALE

(The adult male of Stigmacoccus is not known)

a. Trochanter with several (about eight) sensory pores on each face, tarsus distinctly two-segmented, claw with denticle, tibia with digitule-like setae at apex; costal complex of wing truncate before apex, basal diagonal short; with two clusters of tubular pores dorsally near apex of abdomen. XYLOCOCCINI

aa. Trochanters with fewer (around three) sensory pores on each face, tarsus indistinctly two-segmented, claw without denticle, tibia without digitule-like setae; costal complex of wing tapering to wing apex, basal diagonal, if correctly interpreted, very long, attaining wing apex; with one cluster of tubular pores dorsally near apex of abdomen ---------- MATSUCOCCINI

TRIBE STIGMACOCCINI MORRISON

This tribe, very recently established by the writer (*136, p. 100*), includes only the genus Stigmacoccus. The characteristics given below for this genus will serve adequately as a definition of the tribal characters.

GENUS STIGMACOCCUS HEMPEL

(Pl. 1, A, and figs. 1 and 2)

This genus was established by Hempel (*91, p. 399*) in 1900 with the single included new species *asper*, which thus stands as the type. No other species has ever been correctly assigned here, although Cockerell (*23, p. 233*) incorrectly associated Newstead's genus Perissopneumon with the genus now under discussion.

This genus was currently assigned to the subfamily Dactylopiinae in the sense in which this is recognized in the Fernald Catalogue of the Coccidae of the World (*46*) until Ferris (*51, p. 108*) showed that such a relationship was untenable.

GENERIC CHARACTERISTICS

Habit.—Living during the growing period on the bark of the host, sometimes within ant cartons, but inclosed within an approximately spherical, thick-walled test having an opening at its highest point. Adult female probably retained within the test formed by the earlier stages, and probably ovipositing inside it, although the legs are fully formed.

Adult female.—Flat elliptical, slightly attenuated posteriorly (Hempel); derm membranous and delicate except for a roughly circular to oval, heavily chitinized area at the dorso-anterior apex of the body, this area not inclosing the antennal bases; antennae fully developed, but lightly chitinized, the two basal segments hardly differentiated, forming a large truncate cone with remaining segments continuing from apex of this, with a total of seven to nine segments, all the segments beyond the second bearing one or more differentiated sensory setae, the apex of the second segment bearing four sensory pores; legs fully developed but not heavily chitinized, exhibiting several peculiarities, the trochanter bearing numerous sensory pores (about 14 on each face) instead of the few (two to four) usually present on each face, tibia with a distinct kink and a slight outward bend about one-third of length

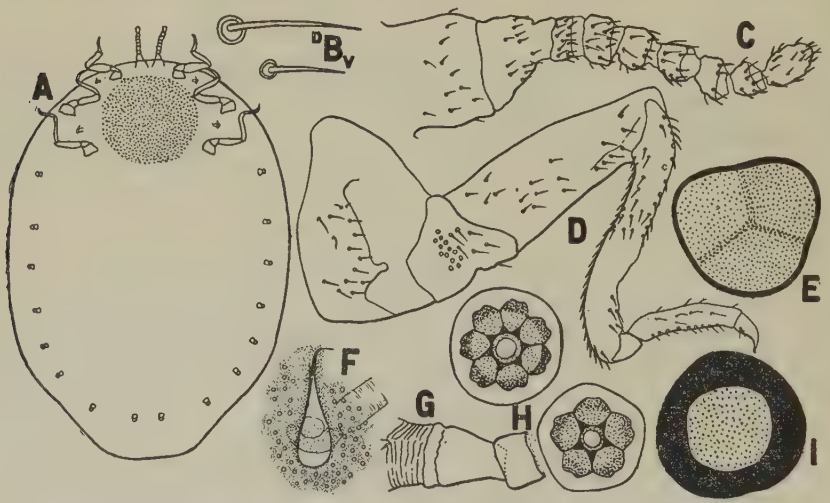

FIG. 1.—*Stigmacoccus asper,* adult female; A, outline, optical section, × 7.5; B, derm setae, dorsal (D) and ventral (V), × 650; C, antenna, × 60; D, leg, × 60; E, faintly trilobate disk pore, × 1,500; F, thoracic spiracle, × 60; G, abdominal spiracle, × 115; H, derm disk pores, × 1,500; I, simple disk pore, × 1,500

from apex, tarsus two-segmented, distinctly curved, claw stout at base, strongly curved, slender at tip, the digitules often, and probably normally, in two pairs on each side of claw, sometimes two and one as in some species of Coelostomidia, each digitule a small, short acute seta; beak present, ordinary, placed close to antennae (Hempel), not observed in any of specimens examined, probably not functional; thoracic spiracles of moderate size, with narrow bar and loose pore cluster around opening, this ovoid, not transverse; abdominal spiracles in eight pairs, opening of each nearly as large as with thoracic, with a narrow collar, then a constriction, then an enlarged atrium, posterior pair close together at body apex, smaller than preceding pairs, all with a few minute pores just within opening and with a scattered group of quinquelocular disk pores around opening; derm pores of two sorts, mostly small disk pores with large quinquelocular centers, but in addition with considerably larger, usually irregularly shaped pores with lighter central area and darker border, the whole divided into usually three, rarely four parts by faint darker lines, these particularly abundant and closely crowded toward the posterior apex of the body in the area surrounding the genital opening; derm bearing some small, stiff setae, varying in size, some slender, some spinelike, and with even smaller stiff hairs with expanded bases, these nowhere abundant or crowded, stouter

posteriorly; anal tube not certainly located in specimens examined; genital opening connected with an internal tube opening in the middle of a circle of small clusters of quinquelocular disk pores; ventral cicatrices wanting. (See discussion of simple pores.)

Intermediate female (preadult).—Approaching a globular form, derm membranous, except for a small, heavily chitinized circular disk surrounding the anal opening; antennae reduced to small, flat, circular, chitinized plates bearing several setae; legs apparently entirely wanting; beak short and stout conical, at most obscurely two-segmented, probably, but not certainly, with apical sensory setae; thoracic spiracles of moderate size, with circular opening and bar, a double band of polygonal wax pores within opening and a wide circular to oval cluster of tuberclelike pores surrounding the opening; abdominal spiracles in eight pairs, openings nearly as large as in thoracic, with band of polygonal pores within and cluster of tubercular pores around the opening, but without bar, posterior pair very close to anal opening; derm with peculiar unequally

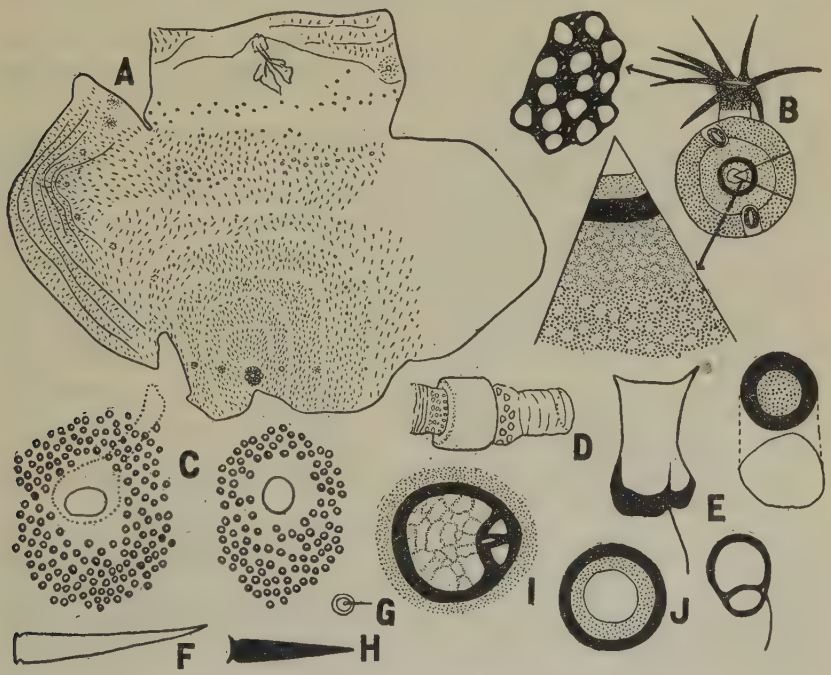

FIG. 2.—*Stigmacoccus asper*, preadult female: A, cast skin, outline, × 12; B, anal tube with attached derm, × 60, with details of structure of internal branch, × 1,500, and of derm plate, × 230; C, thoracic (left) and abdominal (right) spiracles, × 115; D, abdominal spiracle, × 230; E, derm pores, × 1,500; F, derm spine, × 650; G, derm seta, × 650; H, derm spine, × 530; I, derm pore, × 1,500; J, spiracular disk pore, × 1,500

bilocular pores, with many of these invaginated, at the ends of short delicate tubes, and many showing faint transverse lines, dividing each loculus into half, these pores in two distinct sizes, and with numerous simple disk pores, similar to those around spiracular opening in the circular plate surrounding the anal opening; without traces of loculate disk pores at all resembling any of the usual types; derm with numerous, large, rather stout spines, shorter in the midventral abdominal area, abundant over the whole derm except the anterior ventral region; with a comparatively few small, short setae, and with even fewer and smaller hairs; anal tube large, of very peculiar form, cylindrical, with wide band of apparently simple pores near inner end and a series of large tentacles, suggesting those of a squid (six to eight in number), protruding into the body cavity, each tentacle bearing numerous approximately circular simple disk pores; ventral cicatrices not observed, apparently wanting.

Larva.—Not known.

Adult male.—Not known.

The genus is now known to occur in southern Brazil and in British Guiana, both included within the Brazilian subregion of the Neotropical region.

Nothing is known of the life history of the single included species.

TRIBE XYLOCOCCINI COCKERELL

This tribe was established by Cockerell (*17, p. 275*) in 1899 for the reception of all of the genera other than Margarodes that had been associated together to form the subfamily Margarodinae. As here restricted, it includes only the genus Xylococcus and another closely related but only recently described genus.

Tribal Characteristics

Habit.—Living during the growing period in cavities in the bark of the host or in hollow pits formed at the twig axils. Adult female sometimes emerging for oviposition, sometimes remaining and ovipositing inside the cell in which it has developed.

Adult female.—Body rather elongate ovate or elliptical, membranous or with the posterior apex of the abdomen more or less heavily chitinized; antennae either reduced to small cylindrical stubs or elongate, normally nine-segmented, in either case with four sensory pores near base or on second segment; legs reduced to small globular or undifferentiated appendages or normally developed, the trochanters in the last with around eight sensory pores on each face, claw with denticle, claw digitules acute and not attaining claw apex; beak present or wanting or more or less developed; thoracic spiracles with or without bar, with disk pores within atrium, definitely smaller than the abdominal; abdominal spiracles in eight pairs, with disk pores within atrium; derm disk pores present, some simple, some multilocular disk; anal tube well developed, with ring at inner end.

Intermediate female.—Tribal characteristics agreeing with those given below for this stage of the genus Xylococcus.

Larva.—Tribal characteristics agreeing with those given below for this stage of the genus Xylococcus.

Adult male.—Tribal characteristics agreeing with those given below for this stage of the genus Xylococculus.

The adult females of Xylococcus and of the genus here characterized as new, Xylococculus, are very distinct and may be easily separated by the key that follows. No certain basis for separating the intermediate female and the larval stages has been discovered thus far, and no characters in the adult male that can be considered as of significance.

The known distribution of the two genera included here touches the European and Manchurian subregions of the Palaearctic region, and the Californian, Alleghenian, and Canadian subregions of the Nearctic region.

The life histories of the members of the included genera are relatively well known. With one species the life cycle is claimed to require a three-year period for completion.

Key to Genera of Xylococcini

ADULT FEMALE

a. Antennae reduced to short unsegmented tubercles; legs reduced to slight bulges, or, at most, to small, nearly hemispherical tubercles. ..... Xylococcus

aa. Antennae fully developed, elongate, normally nine-segmented; legs well developed, the parts fully formed ..... Xylococculus

The larvae of these two genera do not appear to be separable. The intermediate stages are likewise very similar, and no certain basis for segregating them generically has been obtained from the study material examined.

Genus Xylococcus Löw

(Figs. 3, 4, and 5)

Xylococcus was established as a genus by Franz Löw (*118, p. 271, 274*) in 1882 as a result of his studies on an Austrian species, also described as new by him in the same paper under the name *filiferus*. The present-day conception of the genus is based almost entirely on the work of Hubbard and Pergande (*100*) who discussed at length an American insect which they assigned to Xylococcus. Through the kindness of F. Maidl, of the Natural History Museum of Vienna,

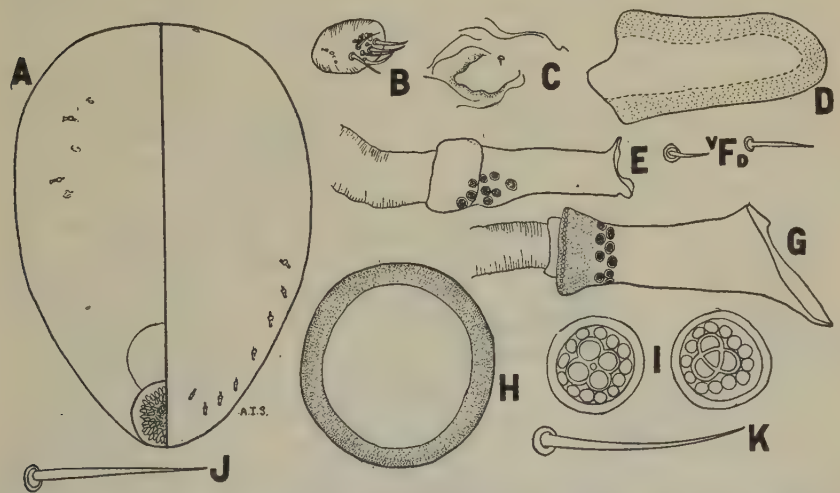

Fig. 3.—*Xylococcus filiferus*, adult female: A, outline of body, dorsal and ventral, with preadult derm plate still attached, × 17.5; B, antenna, × 230; C, leg, × 230; D, spine from preadult derm plate, × 165; E, thoracic spiracle, × 230; F, anterior body setae, dorsal (D) and ventral (V), × 650; G, abdominal spiracle, × 230; H, simple derm pore, dorsal, × 1,500; I, multilocular derm pores, ventral, × 1,500; J, seta from fold near posterior end of body, × 650; K, posterior ventral body seta, × 650

examples of Löw's own specimens have been received and studied and it is therefore now possible to redefine the genus in relation to the North American species commonly assigned to it. On the basis of the generic concepts accepted in this paper, it seems best to group the American species in another genus distinct from Xylococcus. This is characterized later.

GENERIC CHARACTERISTICS

Habit.—As given above for the tribe, in part.

Adult female.—An elongate to elongate ovate sac, broadened more or less anteriorly; posterior apex of body either retaining a chitinized cap from the apex of the preadult cast skin, or itself distinctly chitinized and somewhat wrinkled; antennae developed as short, unsegmented, membranous to definitely chitinized, cylindrical tubercles bearing sensory and other setae at apex and four tiny sensory pores toward base; legs reduced to more or less obviously developed small protuberances from the derm, these appearing as unchitinized

folds or as globular chitinized swellings, apparently bearing a minute claw at apex of each; beak present or lacking, if the first, small, one-segmented, bearing about four apical setae; thoracic spiracles smaller than abdominal, without or with a small narrow bar, with an internal pore collar; abdominal spiracles in eight pairs, each relatively large, with long tube and an incompletely double band of asymmetrical, bilocular-center, multilocular disk pores close to inner end, the apical pair close to anal opening; derm bearing multilocular disk pores having centers varying from oval to quadrilocular and usually numerous (around 16) loculi, these pores more abundant posteriorly, particularly in the genital region; in addition with numerous simple, circular disk pores (possibly ventral cicatrices?), these more abundant and larger on the intermediate area of the body than posteriorly, much less abundant than the loculate disk pores except anteriorly; derm anteriorly with minute setae set in flat bases, these gradually increasing in size posteriorly, some close to the posterior apex quite stiff and stout; anal opening obscured in genotype, in other species apical with a short, stout tube with ring at inner end; no ventral cicatrices. (See under disk pores.)

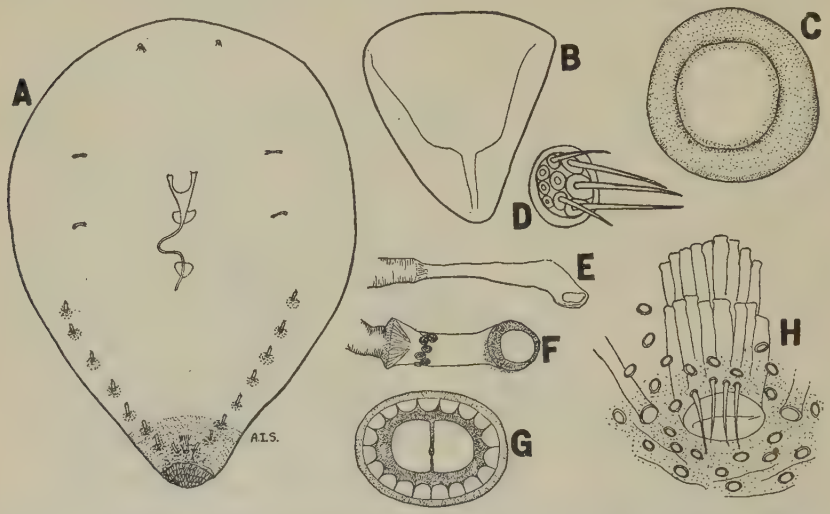

FIG. 4.—*Xylococcus filiferus*, preadult female: A, outline of body, ventral, × 17.5; B, beak, × 230; C, large simple pore, × 1,500; D, antenna, × 650; E, thoracic spiracle, × 230; F, abdominal spiracle, × 230; G, multilocular disk pore, × 1,500; H, anal tube and adjacent region, × 165

Intermediate female (preadult).—Ovate to distinctly top-shaped, broader anteriorly and usually distinctly narrowed to posterior apex, derm usually faintly small areolate, increasingly more strongly chitinized toward posterior apex of body, the area around anal opening heavily chitinized; antennae reduced to flat oval plates bearing several setae, some stout, sensory; legs entirely lacking; beak small, somewhat elongate conical, probably without apical setae, apparently one-segmented; thoracic spiracles much reduced, distinctly smaller than abdominal, no bar developed, no disk pores within atrium; abdominal spiracles in eight pairs, each relatively large, elongate tubular, with a band of multilocular disk pores near inner end, the posterior pair close to the anal opening; derm pores of two types present, one multilocular disk, usually with bilocular center and numerous loculi, the other larger, simple disk pores, closely resembling ventral cicatrices; derm at posterior end of body with some stiff setae set in flat bases; setae elsewhere, if present, small, inconspicuous; no spines or hairs observed; anal opening apical or subapical, anal tube of moderate length, the inner end and normally also the intermediate portion with circles of wax pores set at the inner ends of chitinized invaginated ducts, these rows staggered and overlapping and producing a thick-walled hollow wax tube; no ventral cicatrices. (See under disk pores.) Earlier stages in general similar to that already described.

Larva.—As mounted, uniformly short elliptical, posterior apex heavily chitinized, gradually less so anteriorly, the whole derm in early larva minutely but densely papillate; antennae placed close together, but not contiguous, at anterior apex of head, short, stout, six-segmented, intermediate segments narrow, apical rounded but hardly larger than first or second, bearing some stout sensory setae, second with a single sensory pore; legs of moderate size, bearing a few slender setae, tarsus nearly equal to tibia in length, trochanter with two pairs of sensory pores on each face, claw slender, curved, with distinct denticle, claw digitules slender, distinctly knobbed at apices, exceeding tip of claw; beak uncertain, apparently small and poorly developed, framework of mouth parts large, conspicuous; thoracic spiracles obscure, smaller than abdominal, with faintly developed bar and one disk pore at opening of each; abdominal spiracles in eight pairs, the posterior close to the

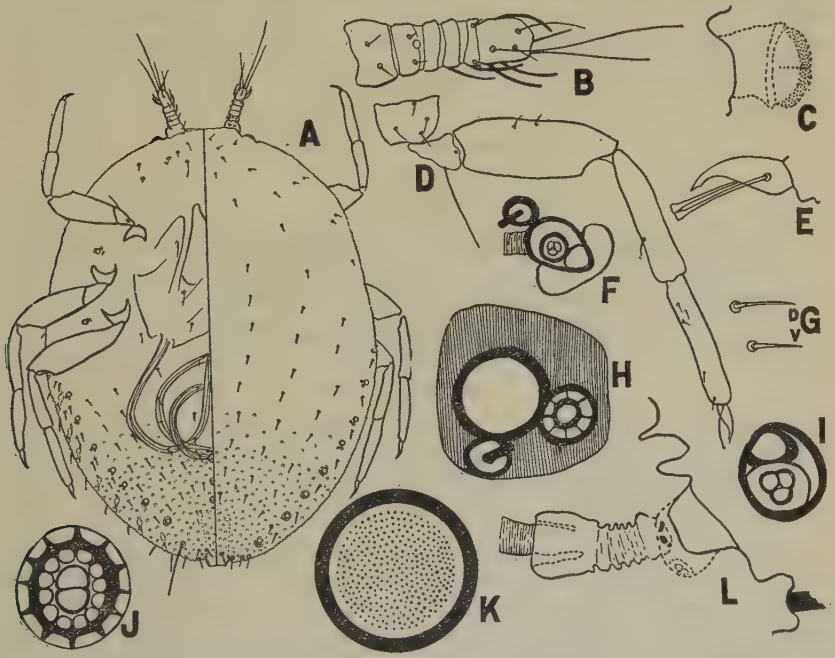

FIG. 5.—*Xylococcus filiferus*, larva: A, outline, dorsal and ventral, × 115; B, antenna, × 460; C, invaginated bilocular disk pore, × 1,500; D, leg, × 230; E, tarsal claw, × 650; F, thoracic spiracle, × 1,500; G, body setae, dorsal (D) and ventral (V), × 650; H, simple pore with disk pore and seta adjacent, × 1,500; I, opening of abdominal spiracle, × 1,500; J, multilocula disk pore, × 1,500; K, single ventral cicatrix, × 1,500; L, abdominal spiracle, × 1,500

anal opening, each slender, elongate tubular with one disk pore in opening and deeply invaginated cup at inner end; derm pores including multilocular disk, with simple center and 7 to 12 loculi, and large, more or less deeply invaginated, bilocular pores, both of these types in marginal and submarginal rows on abdominal segments; derm anteriorly with some scattered minute setae, the margin and posterior end of abdomen with a number of stout spinelike setae, particularly around anal opening; no spines observed, perhaps a few minute hairs with strongly expanded bases present ventrally; with a single pair of short, stout apical setae, hardly more than one-eighth the length of the body; anal opening apical, surrounded by a thin protruding chitinized collar, anal tube stout, not very elongate, inner end with bands of tubular pores corresponding to those of intermediate stages; ventral cicatrices (presumably) in a single median ventral row varying from two to seven in number, on occasion showing fairly plainly narrow lines dividing each into two, three, or four large segments.

Adult male (based on *japonicus* only).—Very closely resembling that of Xylococculus; differing in two observed respects not positively known to be of generic significance: Antennae distinctly more slender and more elongate; penis sheath with a stout transverse quadrate section at base, with the taper starting from this rather than directly from the basal angles.

Two species are definitely included in Xylococcus according to the present arrangement. These are the genotype *filiferus* Löw (*118, p. 271*) from Austria and *X. japonicus* Oguma (*153a, p. 101*), proposed as a new name for the preoccupied *X. alni* Oguma (*153, p. 77*), from Japan. Probably a third species, *X. napiformis* Kuwana (*106, p. 1*), also from Japan, may be retained in the genus with propriety, but no examples of this insect have been available for examination. The two definitely included species agree in the conspicuous reduction of legs and antennae in the adult female, but differ rather strikingly in some other particulars. The adult and preadult stages may be separated by the following keys.

KEYS TO SPECIES OF XYLOCOCCUS

Adult female

a. Antennae distinctly chitinized cylindrical tubercles; legs distinctly chitinized globular protuberances; posterior apex of body more or less definitely chitinized ..... *japonicus* Oguma

aa. Antennae not distinctly chitinized; legs represented only by slight unchitinized bulges in the derm; posterior apex of body remaining membranous, but usually with the chitinous plate from the preadult adherent. *filiferus* Löw

Preadult female

a. Posterior apex of body with a circular plate bearing heavy protuberances and surrounded by a "breaking joint" permitting its detachment at maturity, this to one side of the anal opening, not around it ..... *filiferus* Löw

aa. Posterior apex of body, while heavily chitinized, without any such detachable circular plate ..... *japonicus* Oguma

The seasonal history and habits of the Japanese insect have been discussed in great detail by its describer. The important factor in this connection appears to be the three-year life cycle, with eggs hatching in the spring, larval growth till fall, first molt at this time, the second stage continuing through the first winter and the whole of the second year till the third spring, when a molt occurs and the third stage is reached, and growth occurs during this stage till the end of August, when adult females appear, and after copulation lay eggs during September within the cell inclosing them. These eggs hatch the following spring.

This life history, which was shown to have assisted in the production of the cell in the bark inclosing each insect, through the growth of successive layers of plant tissue around the permanently fixed individual, would seem to be a more logical expectation in the case of the species here assigned to Xylococculus, which develop similar cells, than is the annual cycle implied in the published information on these species.

GENUS XYLOCOCCULUS MORRISON

(Pl. 1, B, and figs. 6, 7, and 8)

This genus was recently established by the writer (*136, p. 101*) for the reception of the North American species that previously

have been assigned to Xylococcus. The genotype is *X. betulae* Pergande (*100, p. 18, 19*), and there are included here in addition *alni* Florence (*54, p. 158*), *macrocarpae* Coleman (*37, p. 198*), and *quercus* Ehrhorn (*43, p. 311*). The paper by Florence (*54*) constitutes an extended contribution on the included species, and this has been supplemented by certain brief comments by Ferris (*51, p. 109*) on the validity of some of these species. The quantity of material available to the writer is insufficient to permit any pertinent remarks on this subject of species validity and this question must therefore remain as left by Ferris.

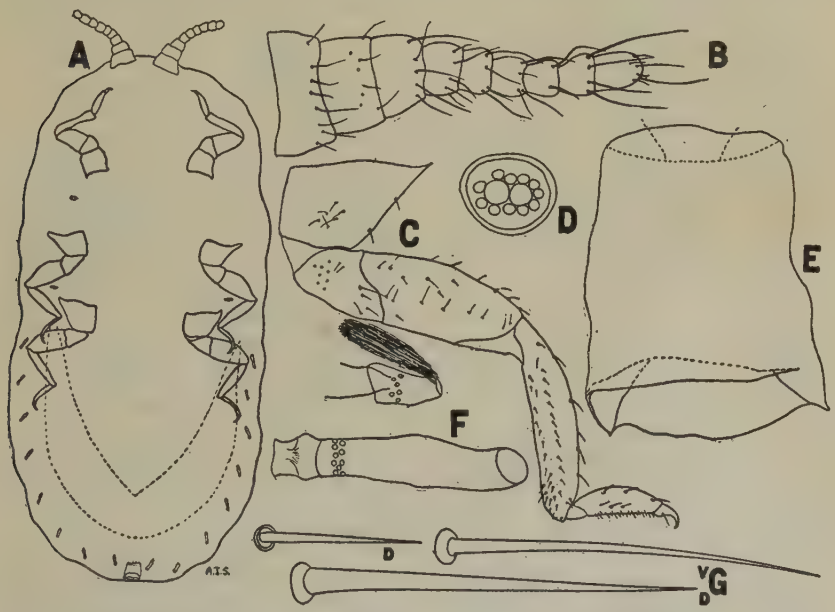

FIG. 6.—*Xylococculus betulae*, adult female: A, outline of body, ventral, × 12; B, antenna, × 60; C, leg, × 50; D, ventral multilocular disk pore, × 1,500; E, anal tube, × 165; F, thoracic (above) and abdominal (below) spiracles, × 120; B, body setae, dorsal (D) and ventral (V), × 650

GENERIC CHARACTERISTICS

Habit.—As given above for the tribe.

Adult female.—When fully distended, elongate elliptical, sides nearly parallel, derm wholly membranous; antennae well developed, normally nine-segmented, the three basal segments forming an enlarged truncated cone bearing the remaining segments at the apex, second segment with several (four) sensory pores, apical segment with some distinctly stouter sensory setae; legs well developed, the trochanters with several (about eight) sensory pores on each face, the setae small or slender, not tending toward stout spinelike, tarsus somewhat obscurely but definitely two-segmented as in Stigmacoccus, claw moderate in size, curved, faintly denticulate within, claw digitules approaching but not attaining claw apex, tips not knobbed; beak and mouth parts wanting to fully developed; thoracic spiracles small, poorly developed, with slightly developed bar, not so large as the abdominal, but with a collar of disk pores; abdominal spiracles relatively large, elongate tubular, with distinct band of asymmetrical multilocular disk pores close to inner end, in eight pairs, the posterior close to anal opening; derm pores of two types, small multilocular disk, with simple to quinquelocular center and numerous small marginal loculi, and somewhat larger, circular disks, sometimes showing very indistinctly the narrow dividing lines of the comparable pores of Stigmacoccus; both sorts of pores more

numerous toward the posterior apex of the body; derm without spines, the setae slender or stout and distinctly spinelike, but with narrow basal collar; no hairs observed; anal opening apical, anal tube short, slightly chitinized, inner end with a narrow, slightly chitinized ring; no ventral cicatrices observed.[9]

Intermediate female (preadult).—Usually ovate to elongate ovate, broader anteriorly; derm somewhat membranous anteriorly, usually faintly and minutely areolate, increasingly more densely and more strongly chitinized toward posterior apex, area around anal opening heavily chitinized; antennae reduced to flat invaginated plates bearing several setae, including some stout, sensory; legs entirely lacking; beak small and short, structure uncertain, probably one-segmented or, at most, indistinctly two-segmented; thoracic spiracles much reduced, smaller than abdominal, bar not developed, not accompanied by a disk pore collar; abdominal spiracles in eight pairs, relatively large, elongate tubular.

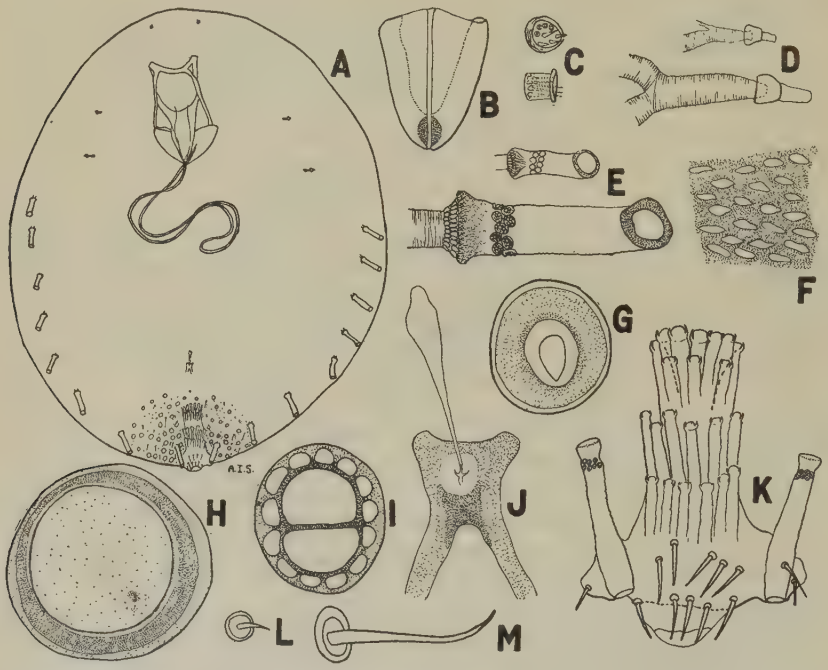

FIG. 7.—*Xylococculus betulae*, preadult female: A, outline of body, ventral, × 30; B, beak, × 120; C, antenna, surface and section, × 230; D, thoracic spiracle, × 120 (above) and × 230 (below); E, abdominal spiracle, × 120 (above) and × 230 (below); F, portion of derm showing areolation, × 530; G, dorsal simple disk pore, × 1,500; H, ventral simple disk pore; × 1,500; I, bilocular center multilocular disk pore, × 1,500; J, Pergande's "brownish organ," × 230; K, anal tube and immediately adjacent spiracles, × 120; L, ventral seta, × 650; M, submarginal seta, × 650

with double band of asymmetrical multilocular disk pores near inner end, posterior pair close to anal opening; derm pores of two types present, one multilocular disk with numerous loculi, mostly circular with rounded to oval bilocular center, these, in one species at least, at the inner end of short invaginated tubes, and the other simple circular disk pores, closely resembling ventral cicatrices, these most numerous on the posterior portion of the body; derm on posterior apex of body, immediately surrounding anal opening, with a few stiff spinelike setae set in flat bases, setae elsewhere small, inconspicuous; no spines or hairs observed; anal opening apical, anal tube of moderate length, the inner end and normally also the intermediate portion with circles of wax pores set at the inner ends of chitinized invaginated ducts, these rows staggered

[9] This statement assumes that the so-called circular simple disk pores have been correctly defined as pores; in appearance they closely resemble small circular ventral cicatrices.

and overlapping, producing a thick-walled wax tube; no ventral circatrices. (See under disk pores.)[10] Earlier stages in general very similar to that just described, smaller, pores, etc., less abundant.

Larva.—Apparently identical with that of Xylococcus in all important characters, apparently even without definite specific characters to separate these larvae from those of Xylococcus.

Adult male.—Of the usual elongate shape, antennal bases placed close together at apex of head, the intermediate area straight or concave in outline, not convex-triangular; both dorsal and ventral aspects of head apex with median chitinized stripe; antennal segments beyond third cylindrical to very

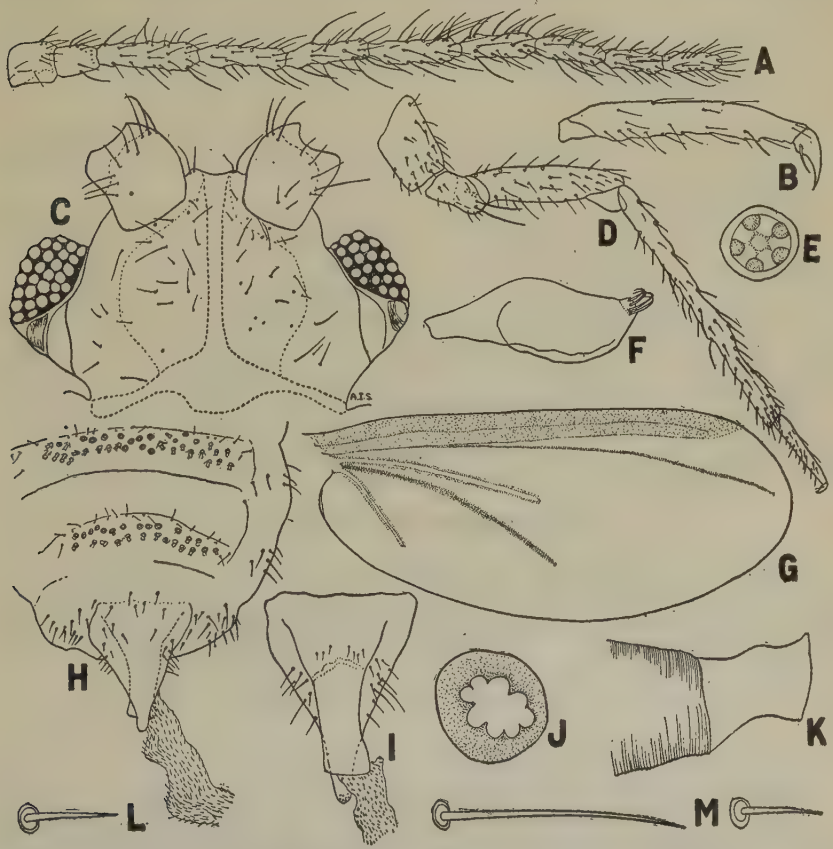

FIG. 8.—*Xylococculus betulae*, adult male: A, antenna. × 60; B, tarsus and claw, × 165; C, head, dorsal, × 115; D, leg, × 60; E, dorsal derm disk pore, × 1,500; F, halter, × 120; G, wing, × 17.5; H, apex of abdomen, dorsal, × 73; I, penis sheath, ventral, × 120; J, single tubular multilocular pore from abdominal bands, × 1,500; K, abdominal spiracle, × 530; L, ventral seta, × 650; M, dorsal setae, × 650

faintly clavate, irregularly nodulose, the setae not in whorls, the segments from the third on gradually decreasing in length, apical shortest; legs moderately slender, the trochanters with numerous (around eight or more) sensory pores on each face, the tarsus rather distinctly two-segmented, claw fairly stout, curved, roughened or faintly denticulate within, the digitules short, acute, not even approaching the claw apex; wing rather narrow, costal complex not continued to wing tip in specimens examined, with an apical diagonal vein running parallel to apex of costal complex, then bending down and con-

[10] Pergande's "brownish organ" (*100, p. 23*) is observable, and appears to be located in the region of the genital opening of the adult. Its function is not known; in addition to the posterior arms there is present anteriorly an elongate duct with clavate end.

tinuing almost to wing apex, this apparently the radial sector of the Comstock-Needham system, basal diagonal vein short, diagonal light folds present, inconspicuous; halteres somewhat expanded, apices each with several (four or more) long curved setae, these not distinctly knobbed at tips; abdomen parallel-sided; with fairly large, brownish, chitinized, transverse segmental plates dorsally and ventrally; no traces of apical or lateral tassels, preapical and preceding segments dorsally with transverse bands of conspicuous, long tubular ducts producing a "tail" of secretion; penis sheath truncate anteriorly, stout conical, tapering nearly uniformly, apex rounded, ventral valve somewhat curved downward and somewhat expanded at tip; penis itself "fleshy," nearly as long as the abdomen, bearing numerous slender and a few stout spines; abdominal spiracles in eight pairs, each opening through an inconspicuous ring; derm with the usual male type of quadrilocular or quinquelocular pores in addition to the long tubular dorsal pores in two clusters, these last with internally crenulated wall, and apparently corresponding loculi at inner end; derm bearing small, rather stiff setae only.

The certainly known distribution for the species here considered as Xylococculus includes only the northern part of the United States and California.

The various stages of the known species have been worked out in much detail, and are described in the papers already cited. Curiously enough, no statement seems ever to have been made regarding the length of the life cycle, a matter of some interest in view of Oguma's observations on the Japanese species attacking Alnus, where a three-year cycle is claimed. By implication, a one-year cycle is found in the North American species of Xylococculus according to the papers of Hubbard and Pergande (*100*) and Florence (*54*).

As previously stated, the available material is not sufficient to permit an attempt at keys for the separation of the different stages of the species which have been assigned to Xylococculus.

TRIBE MATSUCOCCINI MORRISON

Established during the year 1927 (*136, p. 101*), this tribe contains the single genus Matsucoccus Cockerell. The characterization given below for this will serve adequately to define the tribe as well as the genus itself.

Genus Matsucoccus Cockerell

(Pl. 1, C, and figs. 9, 10, 11, and 12)

Matsucoccus is a generic name applied by Cockerell (*28, p. 56*) to the insect described by Kuwana (*103, p. 91; 105, p. 209*) as *Xylococcus matsumurae*. Since the publication of the original description of the genotype, two new species have been described from the United States, and the genus has been treated in detail by Herbert (*97, 98*). A generic synonym is Americoccus, erected by MacGillivray (*119, p. 78*) for one of the species, *fasciculensis*.

GENERIC CHACTERISTICS

Habit.—Living, so far as is now known, only on species of Pinus, the habit varying, one species living during the growing period exposed on the needles, one within the individual needle bundles, and one within flat pustule galls on the twigs.

Adult female.—Body elongate, somewhat broader near the posterior end; derm membranous throughout; antennae placed close together at anterior apex of head, not quite contiguous, nine-segmented, the two basal enlarged, very

incompletely chitinized, segment 2 with three small sensory pores, the remaining segments distinctly broader at distal margin, and those beyond the fourth or fifth bearing a pair of very stout sensory setae in addition to slender setae, apical segment almost conspicuously truncate, all beyond second rather distinctly reticulate or imbricate-reticulate; legs stout, the parts not fused, and bearing a few small setae, trochanter with several (five to eight) sensory pores on each

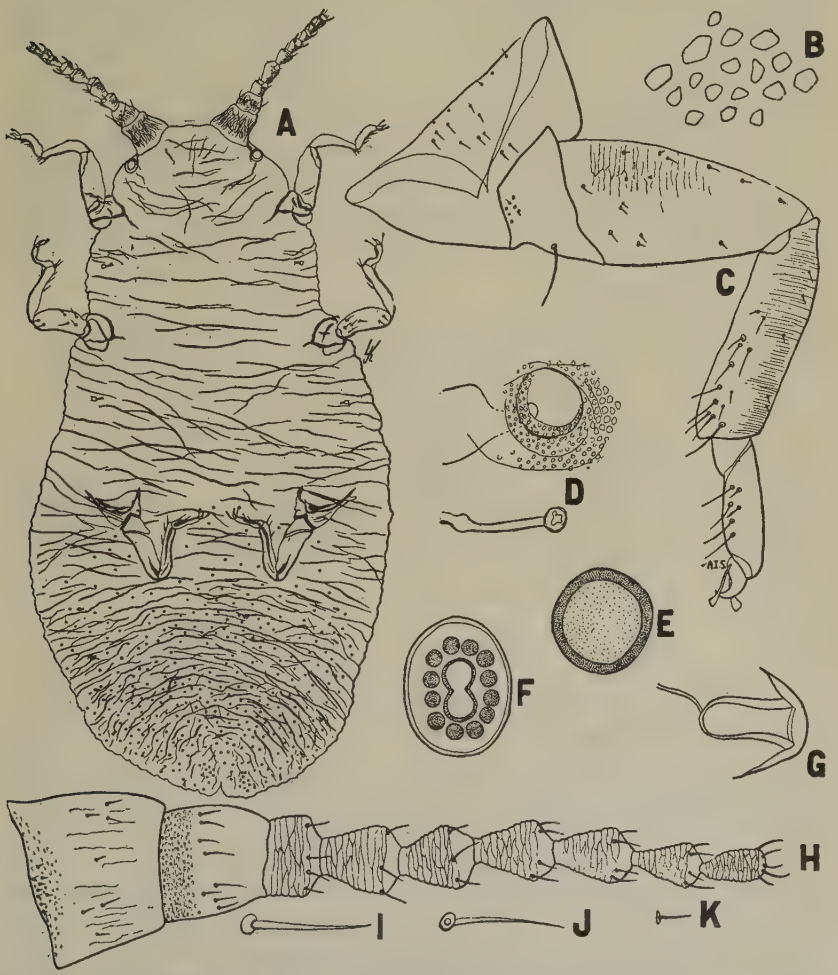

FIG. 9.—*Matsucoccus matsumurae*, adult female: A, outline of body, ventral, × 50; B, faint dermal areolation toward posterior apex of body, × 1,500; C, leg, from American specimen, × 120; D, spiracles, thoracic above, surrounded by derm areolations, not pores, and abdominal below, × 230; E, disklike simple pore, × 1,500; F, bilocular-center multilocular disk pore, × 1,500; G, same, optical section, × 1,500; H, antenna, from American specimen, × 120; I, posterior ventral seta, × 650; J, anterior seta, × 650; K, submarginal seta, × 650

face, tibia usually somewhat curved, tarsus rather distinctly two-segmented, the basal segment short, claw stout, curved rather strongly, bearing two large digitules, these strongly knobbed and definitely surpassing the apex of the claw; framework of mouth parts present or wanting, beak, at most, represented by small liplike protuberances between anterior coxae; thoracic spiracles set well out near margin, opening circular, without bar, without pores, of moderate size;

abdominal spiracles in seven pairs, the anterior missing, smaller than thoracic but quite evident, each with circular opening, without disk pores; derm pores of a single general type, disk with bilocular centers and usually, but apparently not always, with ring of loculi around this center, these loculi when present as many as 16 in number, the pores or their centers invaginated to very deeply invaginated, actually tubular; derm, at least in the abdominal region, with transverse rows of circular, apparently disklike simple pores, these strongly resembling small ventral cicatrices; derm with some setae of moderate size in ventral segmental rows on abdomen, and with smaller, but not minute, setae on both surfaces; anal tube not definitely developed, not located, possibly present and very delicate and membranous with apical opening; no ventral cicatrices. (See under pores.)

Intermediate female (preadult).—Stout elliptical, nearly circular to elongate elliptical, or somewhat elongate-ovoid; derm more or less distinctly chitinized and brown at maturity; antennae apparently, and perhaps actually, lacking; legs wholly lacking; beak slightly developed, one-segmented; thoracic spiracles without bar, moderate in size but conspicuous, due to presence of a well-developed circular pore plate or large multilocular disk pore inside the opening of each; abdominal spiracles in seven pairs, the anterior lacking, hardly differentiated in appearance from the thoracic; body without other pores and apparently without setae; anal tube small, not or hardly chitinized, often not to be located; no ventral cicatrices.

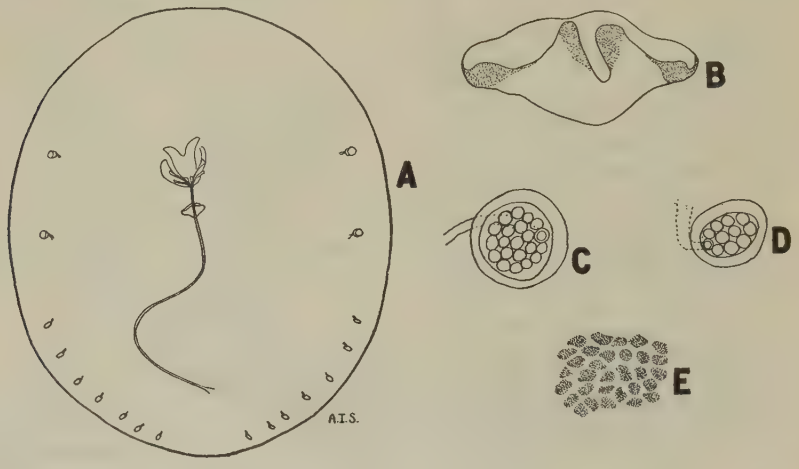

FIG. 10.—*Matsucoccus matsumurae*, preadult female: A, outline, ventral, × 60; B, beak, probably distorted, × 650; C, thoracic spiracle, with disk pore plate, × 650; D, abdominal spiracle, × 650; E, small section of derm showing areolation, × 165

Larva (based chiefly on genotype).—Body elongate elliptical, more or less attenuated at extremities; derm membranous; antennae usually nearly contiguous at anterior apex of head, six-segmented, the third and fifth very short, others elongate, the fourth and sixth bearing stout sensory setae, the sixth with a much smaller, constricted, terminal prolongation, set off and almost appearing as a distinct segment; legs stout, the anterior slightly larger than the others, trochanter incompletely separated from the femur, bearing a single relatively long seta, and apparently two sensory pores on each face, remaining parts with very few setae, claw slender, only slightly curved, claw digitules slender but distinctly knobbed at apices, definitely exceeding tip of claw, no claw denticle; framework of mouth parts large, beak small, one-segmented, very stout conical, placed opposite middle legs; thoracic spiracles small, poorly developed, without trace of bar; abdominal spiracles in seven pairs, about the same size as thoracic but much more conspicuous, opening through small chitinized marginal tubercles, none of the spiracles in any way associated with definitely formed disk pores; no derm disk pores present; with a pair of apical setae about one-sixth the length of the body, this pair accompanied by another much shorter, but still

evident; abdomen, at least, with a submarginal row of small circular disks, these possibly the bases of minute setae; anal opening very obscure, not certainly observed, apparently small, precisely apical and without chitinized tube or other internal evidence of its existence; no traces of ventral cicatrices.

Adult male (genotype only).—Of the usual elongate shape; antennae placed close together, the head hardly exposed between them, the two basal segments very stout, the remainder elongate, slender, cylindrical or slightly larger toward tips, 10-segmented, each segment bearing several slender setae; head short and compound eyes large, giving the head a transverse appearance, rather than the usual quadrate form; legs slender, trochanters with about three sensory pores on each face, the parts, particularly the tarsi, more or less distinctly imbricate or imbricate-reticulate, tarsus one-segmented or, perhaps more properly, indistinctly two-segmented, the short basal segment separated only by a diagonal impressed line, claw fairly stout, the apical portion rather strongly curved, no denticle, digitules large, strongly knobbed, the tips plainly exceeding the apex of the claw; wings elongate, narrow, the costal complex continued to the wing apex, the single diagonal, if correctly interpreted, arising rather close to the wing base and continuing down the approximate

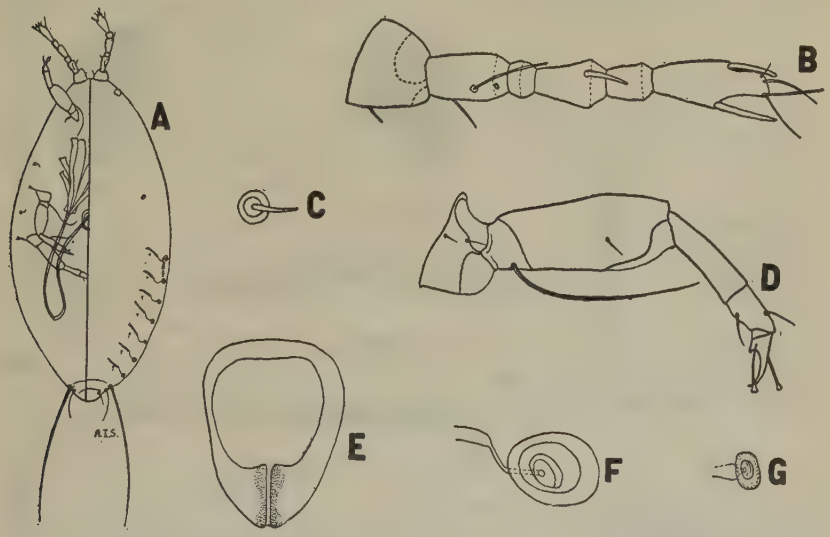

FIG. 11.—*Matsucoccus matsumurae*, larva: A, outline, dorsal and ventral, × 120; B, antenna, × 650; C, dorsal seta, × 1,500; D, leg, × 650; E, beak, × 650; F, abdominal spiracle × 1,500; G, thoracic spiracle, × 1,500

middle line of the wing to its apex, here practically joining the apex of the costal complex, the posterior light fold, again if correctly identified, arising very close to the wing base, running sharply diagonally to the wing margin, cutting off an anal lobe; halteres slender, broadest at apex, bearing here several (about six) long, slender, curved setae with very slightly knobbed tips; abdomen membranous, with a few small chitinized patches dorsally, these not at all conspicuous, with no suggestion of apical or marginal lobes, with a single transversely oval cluster of elongate multilocular tubular pores dorsally near the apex of the abdomen; abdominal spiracles not very evident, apparently with seven pairs; with a few very small setae, these hardly evident; penis sheath broad at base, tapering strongly, then gradually to a slender conical, somewhat rounded tip, lower valve slender, elongate, protruding beyond the tip of the sheath proper, and strongly curved downward; with a fleshy penis of uncertain size.

The present known distribution for the three species now assigned to this genus includes Japan and the eastern part of the United States for the genotype, and the western part of the United States for the two others; so, by regions, the distribution stands as the

Manchurian subregion of the Palaearctic region, and the Californian, Rocky Mountain, and Alleghenian subregions of the Nearctic region. Whether the distribution exhibited by the genotype is the result of natural influences or of introduction by man into a new region, and, in the latter case, which region is to be regarded as the true home of the insect, is still a wholly unsolved problem. The insect appears to be widely distributed along the Atlantic seaboard of the United States, in some cases under conditions that suggest that it may be regarded as indigenous to that area. The writer inclines toward the

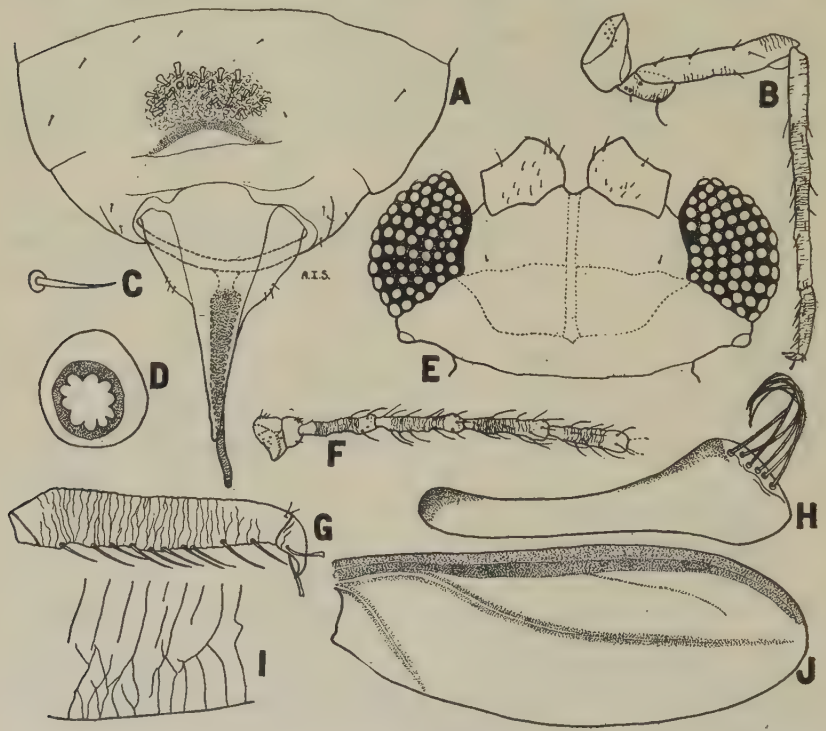

FIG. 12.—*Matsucoccus matsumurae*, adult male: A, apex of abdomen, dorsal, × 120; B, leg, × 60; C, ventral abdominal seta, × 650; D, tubular multilocular pore from abdominal cluster, from above, × 1,500; E, head, dorsal, × 120; F, antenna, basal segments, × 60; G, tarsus and claw, × 230; H, halter, × 230; I, small portion of wing showing pseudonet venation; J, wing showing shape and venation, × 20

hypothesis that it is native to America but that it was introduced into Japan and has become established there.

While the life cycle of the included species appears not to have been worked out in detail for any of the species, Herbert (*97*, *98*) has made several suggestions regarding its probable course. He believes that there is a single generation annually, with larvae hatching and settling in the spring, relatively rapid growth to the adult female stage, and overwintering in the egg stage.

The three included species are the genotype, *matsumurae* (Kuwana) (*103*, *p. 91; 105*, *p. 209*) from Japan and the eastern part of the United States, *acalyptus* Herbert (*98*, *p. 15*) from Idaho, and *fasciculensis* Herbert (*97*, *p. 157*) from California. The male is known

only in *matsumurae*. Various female stages of all the species have been described. These may be separated by the following keys which have been derived largely from the published work of Herbert (*97, 98*). *Kuwania pini* Green (*79, p. 34; 80, p. 172*) is identical with the genotype.

KEYS TO SPECIES OF MATSUCOCCUS

Adult female

a. Derm pores near posterior apex of body with large bilocular center with a circle of small loculi surrounding the central pair; antennae with a pair of stout sensory setae on the sixth and following segments. *matsumurae* (Kuwana)

aa. Derm pores near posterior apex of body large bilocular, but without the accompanying circle of loculi.

b. Antennae with a pair of stout sensory setae on the sixth and following segments ..... *acalyptus* Herbert

bb. Antennae with a pair of stout sensory setae on the fifth and following segments ..... *fasciculensis* Herbert

Intermediate female

a. Body nearly circular in outline or at least very broadly elliptical; last four pairs of abdominal spiracles forming an acute angle with the surface of the body at point of attachment; found within gall-like pits beneath bark of twigs of species of Pinus ..... *matsumurae* (Kuwana)

aa. Body elongate elliptical or somewhat elongate ovoid; abdominal spiracles not as above; not living within gall-like pits in host twigs.

b. All of the spiracles forming an acute angle with the body surface at point of attachment; living inside bundles or fascicles of needles of species of Pinus but not causing any marked abnormal growth. *fasciculensis* Herbert

bb. All of the spiracles perpendicular to the surface of the body at point of attachment; living exposed on needles of species of Pinus. *acalyptus* Herbert

Larva

a. With tiny nipples alternating with spiracles along margin of abdomen; bases of antennae almost contiguous ..... *fasciculensis* Herbert

aa. Without such marginal nipples alternating with the abdominal spiracles.

b. Bases of antennae almost contiguous ..... *matsumurae* (Kuwana)

bb. Bases of antennae relatively widely separated ..... *acalyptus* Herbert

SUBFAMILY STEINGELIINAE MORRISON

This subfamily has just been established by the writer (*136, p. 101*) for two peculiar genera, one Palaearctic, one Nearctic.

SUBFAMILY CHARACTERISTICS

Habit.—So far as known, developing unprotected on the host. Female seeking protected situations for oviposition.

Adult female.—Body very elongate elliptical or slightly broadened behind; derm membranous; antennae well developed, with bases contiguous at apex of head, seven-segmented to eight-segmented, apical segment only with sensory setae, second segment with a single sensory pore; legs well developed, trochanter with two sensory pores on each face, tarsus one-segmented, claw without denticle, claw bearing several (6 to 12) stout knobbed digitules, these exceeding apex of claw; beak and mouth parts present or wanting, the beak, when present, very short conical, one-segmented; thoracic spiracles with bar, without pores within atrium, definitely larger than abdominal; abdominal spiracles in six pairs, these the anterior ones, without disk pores within atrium or otherwise

associated with each spiracle; derm with some circular multilocular disk pores, but without simple pores; derm without spines, disks, or hairs; derm setae relatively few; anal opening subapical, very simple, anal tube wanting; no ventral cicatrices.

Intermediate female (based on one genus only).—Body elliptical to ovoid, more or less chitinized at maturity; antennae reduced to unsegmented plates, bearing one or more sensory setae; legs wanting; thoracic spiracles with bar, without pores within atrium, without tiny setae on derm near opening; with the six anterior pairs of abdominal spiracles developed, these without pores within atrium; derm disk pores wanting; body without spines, hairs, or setae; anal tube subapical, very small and inconspicuous; no ventral cicatrices.

Larva.—Body elliptical or nearly so; antennae five-segmented to six-segmented, with sensory setae on the apical segment only, the bases rather close together at apex of head; legs normal, claw without denticle, the two claw digitules knobbed, exceeding apex of claw; beak inserted opposite middle legs, short conical, one-segmented; thoracic spiracles without bar, without pores within atrium; abdominal spiracles present in the six anterior pairs, without pores within atrium; derm disk pores lacking; with a single pair of somewhat enlarged apical setae; anal tube apical or nearly so, very poorly developed; ventral cicatrices lacking.

Adult male.[11]—Elongate, winged or wingless, thoracic chitinization developed or not; apex of head not acute between antennal bases, antennae slender or stout; compound eyes reduced either to a single facet or to a dorso-ventral row of seven facets; legs without bifurcate setae, trochanters with few (two to three) sensory pores on each face, tarsus distinctly one-segmented, claw without denticle, claw digitules knobbed, somewhat exceeding apex of claw; wings, where present, narrow, with elongate basal diagonal vein, costal complex tapering indistinctly to wing apex, no apical diagonal vein; halteres narrow, with two or three elongate, curved, knobbed setae at apex; penis sheath stout at base, either tapering to an acute entire tip or with two very short, stout lobes overlapping at tips, the lower valve elongate, slender, curving strongly downward and extending well beyond the tip of the sheath proper; disk pores wanting or poorly developed.

A single tribe is included in this subfamily.

TRIBE STEINGELIINI MORRISON

This tribe has been erected by the writer (*136, p. 101*) for the two genera Steingelia and Stomacoccus.

Tribal Characteristics

The characterization of the subfamily, as given just above, serves adequately for the tribe as well.

The distribution of the tribe, as constituted, includes, first, northwestern continental Europe and England, that is, the European subregion of the Palaearctic region; and, second, the Californian subregion of the Nearctic region.

The life cycle of the included forms is not accurately known.

Keys to Genera of Steingeliini

ADULT FEMALE

a. Antennae normally eight-segmented ..... Steingelia
aa. Antennae normally seven-segmented ..... Stomacoccus

(The intermediate female stage of Steingelia is unknown.)

LARVA

a. Antennae normally six-segmented ..... Steingelia
aa. Antennae normally five-segmented ..... Stomacoccus

[11] See footnote 12, p. 57.

ADULT MALE

a. Winged; eyes composed of a vertical row of facets on each side of head; penis sheath very stout, the tip bilobed ..... Steingelia
aa. Wingless; eyes with a single facet; penis sheath with an elongate, slender, entire tip ..... Stomacoccus

Genus Steingelia Nassanow

(Figs. 13 and 14)

First erected by Nassanow (*139, p. 345*) in 1908 for a single species, *gorodetskia*, the genus and species have also received extensive treatment from Green (*69, p. 197; 71, p. 175; 72, p. 268; 73, p. 115; 74, p. 24; 76, p. 211*), in part under the name *Kuwania britannica*.

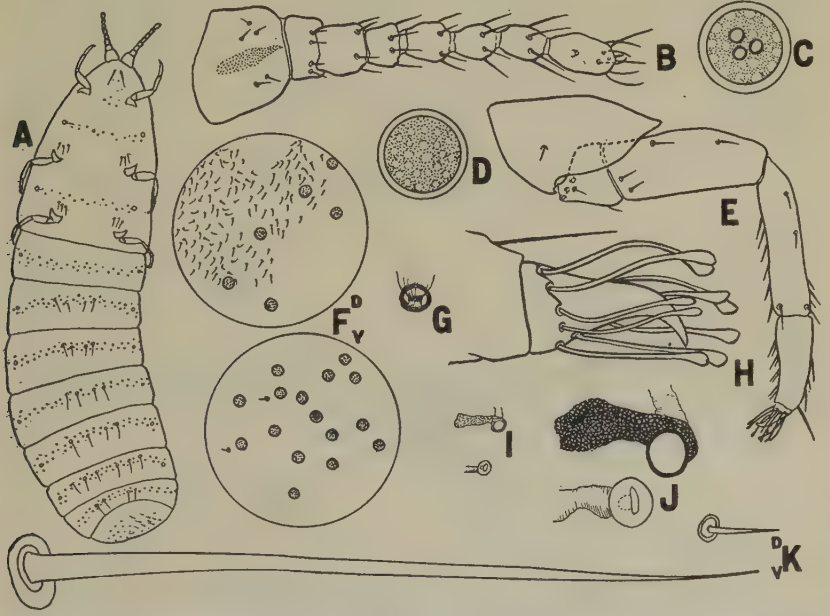

Fig. 13.—*Steingelia gorodetskia*, adult female: A, outline, ventral, × 17.5; B, antenna, × 115; C and D, derm disk pores, × 1,500; E, leg, × 115; F, sections of derm dorsal (D) and ventral (V), near apex of abdomen, × 230; G, anal opening, × 165; H, claw × 650; I, thoracic and abdominal spiracles, × 60; J, the same, × 230; K, largest dorsal (D) and ventral (V) setae, × 650

Although not a portion of its published history, it has been a matter of much interest to the writer to note that Theodore Pergande had indicated this insect as representing an undescribed genus as early as 1898, on the basis of specimens from birch obtained in Prussia.

GENERIC CHARACTERISTICS

Habit.—As given in the subfamily characterization.

Adult female.—Of moderate length, but narrow, slightly broader through the posterior abdominal region; derm membranous throughout; antennae contiguous at base, placed at extreme anterior apex of head, eight-segmented, the basal segment much enlarged, very incompletely chitinized, the remaining segments tapering slightly, somewhat indistinctly imbricated, apical longest of these, elongate ovoid, only the apical bearing stout, definitely differentiated sensory

setae; legs stout, bearing a few setae, the trochanter short, with three sensory pores on each face, tarsus stout, one-segmented, claw stout at base, somewhat curved, without denticle, base of claw with several (about 12) knobbed digitules, these surpassing the claw apex; presence of beak suggested by a few folds between anterior legs, mouth parts sometimes more or less developed; thoracic spiracles with circular opening and narrow, elongate bar, no disk pores in intimate association; abdominal spiracles in the six anterior pairs, likewise with circular opening, distinctly smaller but still evident, not intimately associated with disk pores; derm pores of one type only, fairly numerous, but nowhere crowded, in a cluster on head, in transverse segmental rows on the thorax and abdomen, more numerous and more generally distributed at posterior apex of body; derm ventrally with some quite large setae, these near coxae and in

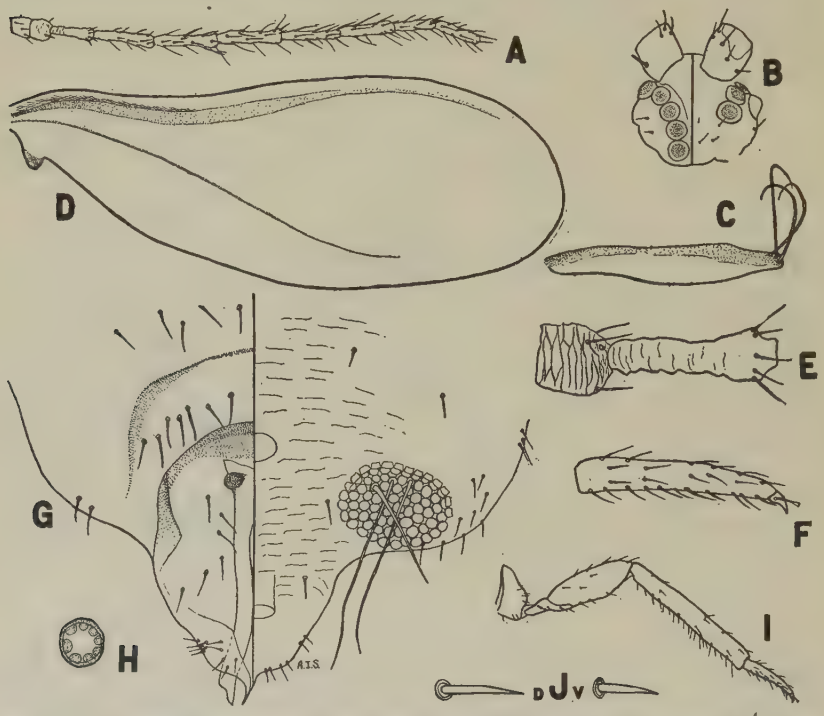

FIG. 14.—*Steingelia gorodetskia,* adult male (based on specimens identified by E. E. Green): A, antenna, × 60; B, head, dorsal and ventral, × 120; C, halter, × 230; D, wing, × 60; E, second and third antennal segments, × 230; F, tarsus and claw, × 230; G, apex of abdomen, dorsal and ventral, × 230; H, derm disk pore from marginal cluster, × 1,500; I, leg, × 60; J, derm setae, dorsal (D) and ventral (V), × 650

transverse segmental rows on the abdomen, and with additional, much smaller, inconspicuous setae on both surfaces; no spines or hairs; anal opening nearly apical, small, circular, with only a small, short internal tube; no ventral cicatrices.

Intermediate female.—Not known.

Larva.—No specimens available. With the following characteristics according to published descriptions: Oval; antennae six-segmented, otherwise very similar to those of Stomacoccus; legs much as in Stomacoccus, claw with two knobbed digitules; beak broad; thoracic spiracles well developed; abdominal spiracles obscure, if present; derm pores uncertain; with long lateral setae opposite anterior legs, and with pairs of fairly long apical setae; probably with some minute setae on derm; anal tube and ventral cicatrices uncertain, the last probably wanting.

Adult male (based on specimens determined by Green)[12].—Of the usual elongate shape; antennae 10-segmented, placed close together at apex of head, two basal segments large, imbricate-reticulate, remainder elongate, slender, nearly cylindrical, somewhat nodulose, fourth somewhat the longest, setae not numerous or long, fairly stout; compound eyes represented by a single, nearly vertical row of seven large round facets on each side of head; ocelli present on a slight protuberance behind the second and third of the dorsal facets; legs fairly elongate, trochanter with three sensory pores on each face, parts, except tarsus, imbricated, this with large reticulations, distinctly one-segmented, claw stout, slightly curved, with two strongly knobbed digitules barely exceeding claw apex; wings narrow, hardly shaded, with basal diagonal only developed, this not very distinct, but extending well toward wing margin, costal complex continued very vaguely toward apex of wing; halteres elongate, narrow, with two to three long, slender, broadly hooked setae at apex; abdomen slightly expanded, presence of abdominal spiracles not demonstrated with certainty; margin of abdomen on each side with seven small clusters of very faintly loculate pores, and with a much larger apical cluster, composed of more distinctly loculate pores surrounding a pair of elongate stout setae, as in Pseudococcus and other genera; with transverse segmental rows of stout, moderately elongate setae; penis sheath large, stout, and broad, anterior opening very large, apical section small, abruptly constricted, terminating in two short, but slender, contiguous prongs, ventral valve slender, curved downward, but short, barely exceeding apex of sheath, anterior hinged section likewise short, ventral derm immediately anterior to sheath with a transverse chitinized plate broadly interrupted medially; most of abdominal segments exhibiting transverse, indistinctly chitinized plates, and much of abdomen faintly transversely imbricated.

The single species included here, *S. gorodetskia*, is known from the northern portion of the European subregion of the Palaearctic region, the political divisions including Russia, Germany (Prussia), and England.

The life history is not at all well known, and the intermediate female stages still await discovery. According to Green, adult males appear in May in England, and ovisacs are formed by the female and oviposition takes place in June. Green also suggests that there may be a prolonged period of growth in the intermediate stages.

Genus Stomacoccus Ferris

(Figs. 15, 16, 17, and 18)

This genus was established by Ferris (*47, p. 375*) in 1917 for the reception of a much simplified margarodine form found in California on sycamore. Neither the type species, *platani*, nor any other species properly assignable to this genus has as yet been reported from any other locality.

GENERIC CHARACTERISTICS

Adult female.—Small in size, body strongly elongated, somewhat broader behind; derm membranous throughout; antennae seven-segmented, bases contiguous at apex of head, the basal segment much enlarged, very incompletely chitinized, intermediate segment distinctly broader at apex than at base, apical

[12]Although these males are regarded by Mr. Green as quite certainly belonging to this genus and species, the writer remains, after extended study of both adult and immature male stages, undecided as to their true status. The circumstantial evidence connected with their discovery strongly favors Green's opinion, but they have never been taken actually mating with the adult females, and the morphological evidence, from present knowledge, strongly favors the view that this male coccid is in reality that stage of a representative of some other group of coccids. Unfortunately, there is no positive knowledge as to the distinctive morphological characteristics of males of other coccid families and subfamilies, so its status can best be considered as somewhat uncertain pending the acquisition of additional data.

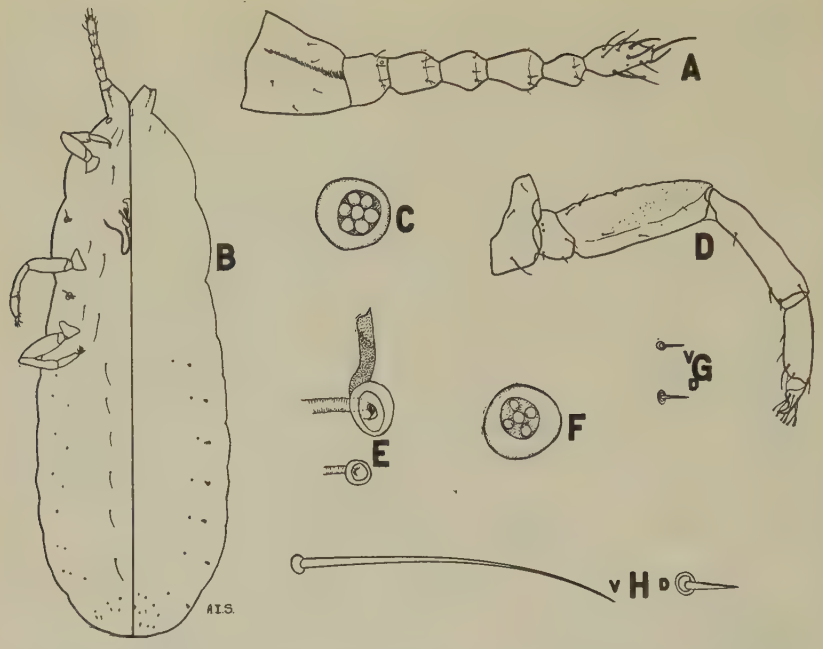

FIG. 15.—*Stomacoccus platani*, adult female: A, antenna, × 230; B, outline, dorsal and ventral, × 60; C, disk derm pore, × 1,500; D, leg, × 230; E, spiracles, thoracic above, abdominal below, × 650; F, ventral disk derm pore, × 1,500; G, small body setae, near apex of abdomen, dorsal (D) and ventral (V), × 650; H, longer ventral (V) and dorsal (D) setae, × 650

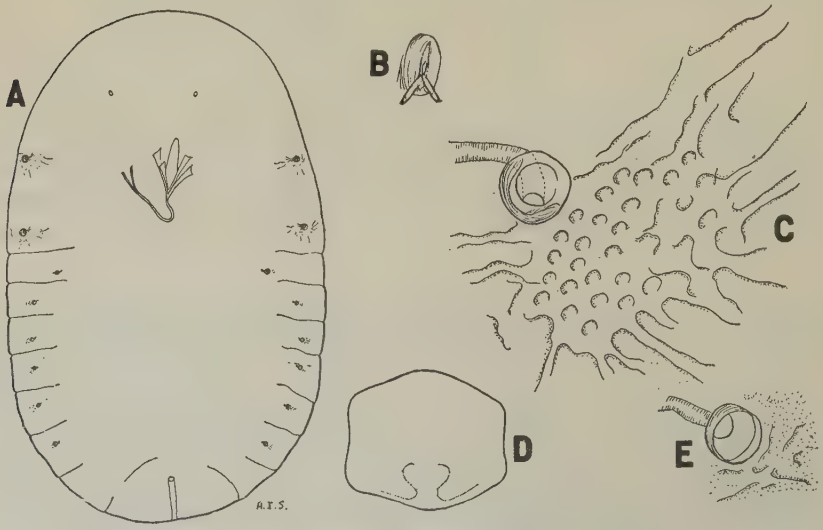

FIG. 16.—*Stomacoccus platani*, preadult female: A, outline of body, optical section, × 165; B, antenna, × 1,500; C, thoracic spiracle and adjacent area, × 1,500; D, beak, × 650; E, abdominal spiracle and adjacent area, × 1,500

nearly as long as basal, but most slender of any, all segments except first very faintly imbricated, only the terminal with stouter and larger sensory setae; legs rather short and stout, trochanter and coxa almost united, other parts distinct, tarsus one-segmented, claw stout, curved, bearing a number (about six) of stout, distinctly knobbed digitules surpassing the apex of the claw; mouth parts developed, beak hardly definitely formed, at most one-segmented; thoracic spiracles of moderate size, opening circular, with narrow bar, with single disk pore on derm behind opening of each, none within; with six pairs of small,

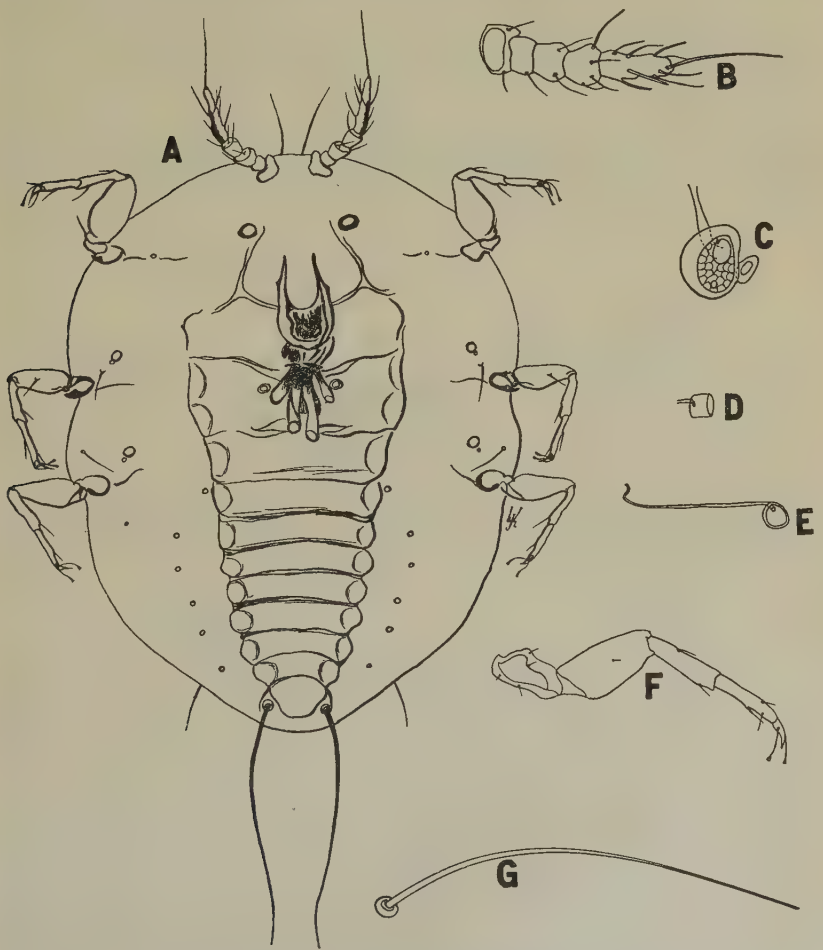

FIG. 17.—*Stomacoccus platani*, larva: A, outline of cast skin, × 330; B, antenna, × 530; C, thoracic spiracle, × 1,500; D, abdominal spiracle, from side, diagrammatic, × about 1,500; E, same, × 1,500; F, leg, × 530; G, long marginal seta from near antenna, × 1,500

simple, inconspicuous abdominal spiracles, these the anterior pairs, each opening placed between two well separated disk pores, but these not obviously associated with the spiracle; derm pores of a single multilocular disk type, small, with small circular center and four to six large loculi, more numerous toward the posterior apex of the body; with pairs of relatively long and large setae ventrally on head, opposite each coxa, and near the median line of each abdominal segment, in addition with a few minute setae both dorsally and ventrally, these occurring most abundantly toward the posterior apex of the abdomen; without spines and apparently without hairs; anal opening subapical, circular,

surrounded by a slightly chitinized line, without definitely chitinized internal tube; no ventral cicatrices.

Intermediate female (preadult).—Small, stout, elliptical, flattened, very slightly chitinized at maturity; antennae reduced to tiny oval plates, each bearing a single sensory seta; legs entirely lacking; beak barely developed, hardly definitely formed; thoracic spiracles of moderate size, with circular opening, very slender bar, and no pores, the derm around each spiracular opening rugose and denticulate; abdominal spiracles in six anterior pairs, as in adult, smaller than thoracic, each without pores, but with a small rugose area near opening; derm, so far as can be determined, wholly without pores of any kind and wholly without setae as well as without spines or hairs; anal opening subapical, with a distinct but shallow groove running from it to the body apex, the opening itself circular, with very slightly developed, short, internal tube; no traces of ventral cicatrices.

Larva (based on cast skins only).—Elliptical, probably elongate; antennae five-segmented, the basal broadest, the terminal much the longest and bearing a long apical seta in addition to others, the third and fourth moniliform; legs small, stout, trochanter and femur apparently fused, claw elongate, slender,

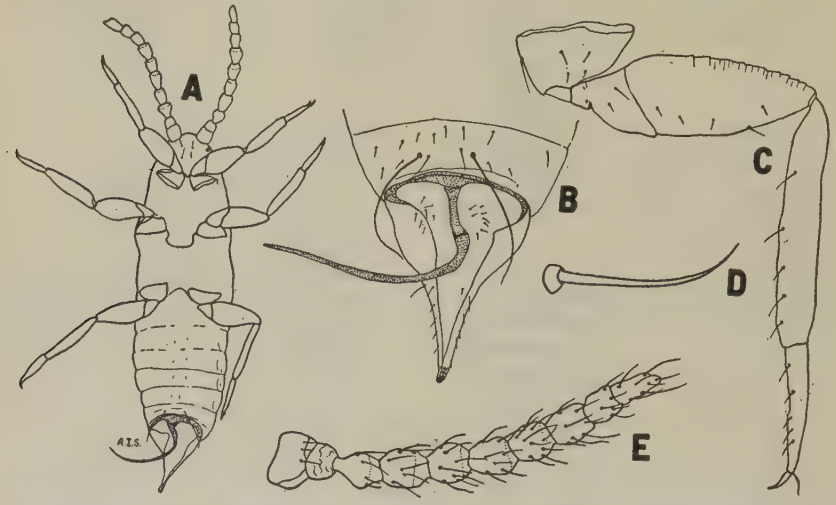

FIG. 18.—*Stomacoccus platani*, adult male: A, outline, ventral, × 60; B, apex of abdomen, ventral, × 165; C, leg, × 230; D, ventral seta, × 1,500; E, antenna, × 165

slightly curved, bearing two stout knobbed digitules exceeding apex of claw; beak barely formed; thoracic spiracles small, without bar, opening circular, a minute seta or simple pore at the mouth of each; abdominal spiracles much smaller, but distinct, in six pairs as in adult, the anterior set further dorsally as in intermediate stages; without derm pores; with a very few setae (one near each coxa, for example), with a single pair of enlarged apical setae, these much shorter than the body; anal opening simple, almost apical, the tube small, short, simple; no traces of ventral cicatrices.

Adult male.—Elongate, slender, membranous throughout, wings wanting, thorax not enlarged or chitinized; antennae and legs relatively large and conspicuous, antennae about half length of body, 10-segmented, the segments stout, the third very strongly constricted at base, the apical slightly the longest, all segments beyond third bearing a number of rather stout setae; eyes each reduced to a single facet placed behind base of antenna; no ocelli (or eyes actually lacking, ocelli present); legs rather stout, no fusion of parts, trochanter with two pores on each face, tarsus distinctly one-segmented, claw slender, slightly curved, without denticle, bearing two slender, knobbed digitules barely surpassing the tip of the claw; abdomen tapering strongly toward tip; with a few slender setae; apparently wholly without pores; abdominal spiracles uncertain; penis sheath of peculiar construction, broad at base and with the sheath

proper tapering to a sharply conical point, lower valve narrow and slender, distinctly longer than upper, strongly curved downward, and acutely pointed at tip, hinged at base to a short bar running to base of sheath.

The known distribution of this genus includes only the coastal region of central and southern California, hence only the California subregion of the Nearctic region.

The life cycle is not known. According to incomplete observation and conclusions by Ferris (*47*), the cycle must be very short.

SUBFAMILY MARGARODINAE COCKERELL

The subfamily name Margarodinae seems to have been proposed first by Cockerell (*17*, *p. 275*) in 1899, when he attempted to develop a series of keys to the genera and higher groups of the Coccidae. One of the two tribes proposed by Cockerell in this publication is here removed to form the nucelus of another subfamily. The other is retained, and to it are added two other tribes, newly erected, but including genera already well known.

SUBFAMILY CHARACTERISTICS

Habit.—Living during the growing period relatively unprotected in crevices in the bark of the host or within very hard, thin-walled tests in loose sandy soil adjacent to the roots of plants. Females seeking protected situations and producing a mass of white secreted wax threads at oviposition, or, in one tribe, ovipositing within an internal marsupium.

Adult female.—Body stout elliptical, almost circular, to elongate elliptical; derm membranous to rather heavily chitinized over entire exposed area; antennae fairly well to very well developed, 6-segmented to 10-segmented (in one species apparently 14-segmented to 16-segmented), basal segments more or less distinctly enlarged, mostly with stouter sensory setae on both apical and preapical segments, second segment with one to several (six) sensory pores near apex; legs well developed, the anterior very much enlarged in one tribe, fitted for digging, trochanters with several to many (4 to 16) sensory pores on each face, tarsi one-segmented, tarsal claw with or without a conspicuous denticle, tarsal digitules acute at tips, not attaining apex of tibia; beak wanting or sometimes present and fairly well developed, at most one-segmented; thoracic spiracles with or, rarely, without bar, with or, rarely, without disk pores within atrium, definitely larger than or, rarely, about equal to the abdominal in size; abdominal spiracles in four to eight pairs, if less than eight, then the posterior lacking, each completely developed spiracle with disk pores within atrium; derm bearing multilocular disk pores, varying in details; derm with or without stout spines, without circular disks, with or without hairs, and with setae, these sometimes so abundant as to give the specimen possessing them a densely hairy appearance; anal opening apical or subapical, tube, at most, small with somewhat developed ring at inner end, often not visibly developed; no ventral cicatrices.

Intermediate female.—Body globular to irregularly elliptical, or ovoid; derm membranous to more or less chitinized; antennae reduced to small plates, sometimes more or less invaginated, bearing one or more stout sensory setae; legs wholly lacking; beak small, stout conical, at most one-segmented; thoracic spiracles without or, rarely, with bar, with disk pores within opening of each, and each with a few, one to several, very tiny setae, set in relatively large but very flat collars, outside or behind the opening; abdominal spiracles in four to eight pairs, if less than eight, then the posterior lacking, each fully developed spiracle with pores within atrium; derm with or without multilocular disk pores; derm without spines or hairs and with very few setae, these sometimes confined to those next to thoracic spiracular openings; anal opening apical or subapical, small, inconspicuous; tube wanting or only slightly developed; ventral cicatrices present or apparently wanting.

Larva.—Body elliptical to very elongate, parallel-sided; derm membranous; antennae mostly stout, four-segmented to six-segmented, apical only, or, rarely, the preapical also, with stouter sensory setae; legs normal, or the anterior pair much enlarged, or, rarely (one species), the anterior pair only retained,

the others lacking, claw with or without denticle, claw digitules lacking (one genus) or acute or blunted, but not attaining claw apex, or knobbed and surpassing claw apex; beak small, short to medium conical, at most indistinctly two-segmented; thoracic spiracles without, or, rarely, with bar, with pores within atrium; abdominal spiracles presumably in six to eight pairs as in adult, frequently very difficult to locate and count correctly, with or without pores within atrium of each; derm with, or, more frequently, without multilocular disk pores; derm without spines, without hairs, and with relatively few setae, with one or two pairs of somewhat enlarged apical setae; anal opening apical or subapical, the tube, at most, not very well developed, no ring at inner end; a single small, circular, ventral cicatrix present or wanting.

Adult male.—Of the usual elongate shape, but stouter than with many other groups; apex of head between antennal bases more or less acute; antennae usually simple, rarely (one genus) conspicuously pectinate and seven-segmented, usually 10-segmented, but segments reported as varying from 9 to 13 in number, stout or slender, the third segment shortest or the apical shortest; legs well developed, unusually stout in one tribe, with the anterior pair much enlarged and fitted for digging, otherwise normal, not bearing bifurcate setae, trochanter with few to many (4 to 15) sensory pores on each face, tarsi in one tribe one-segmented, otherwise two-segmented, claw without or, rarely, with denticle, digitules acute, not attaining tip of claw; wings stout or somewhat narrowed, the basal diagonal long, costal complex various, tapering and attaining apex, tapering but not attaining apex, or truncate well before apex, apical diagonal present or wanting; halteres broad to very broad, with a single or two apical setae, these short, stout, acute at tip, very different from those found in other subfamilies; abdomen with or without heavily chitinized transverse plates, with one or two clusters of subapical, dorsal, tubular pores; penis sheath stout at base, mostly tapering strongly, entire or bilobed at apex, the lower valve short or approximating the length of the sheath proper, and curved downward and somewhat enlarged at apex, or even more elongate, and slender, at apex; derm of abdomen with or without disk pores.

The distribution of this subfamily, as here constituted, is very wide, including one or more subregions of every one of the six major geographical regions.

There is no detailed information available regarding the life history of any of the included species. It seems possible that the members of one of the included genera, Margarodes, have a relatively short or a long life cycle in direct correlation with the ecological conditions to which they are subjected.

The subfamily has been expanded from its ordinary usage to include not only those genera with much enlarged anterior legs, here considered as a tribe, Margarodini, but certain other genera which seem to show some relationship in other characters, although lacking the enlarged anterior legs. These additional genera are grouped in two tribes, Kuwaniini, including Kuwania and Neosteingelia, and Callipappini, including Callipappus only. So far as the stages are known these tribes may be separated by the following keys.

KEYS TO TRIBES OF MARGARODINAE

Adult Female

a. Anterior legs much larger than the other pairs, very stout, with very heavy claw, the whole adapted for digging; body stout elliptical, often nearly circular in outline in microscopic mounts ..... MARGARODINI

aa. Anterior legs closely approximating others in size, not unusually stout; body elliptical or, more often, elongate elliptical.

b. Body rather heavily chitinized at maturity, the posterior abdominal segments (beyond the third) deeply invaginated from the apparent posterior apex to form a large internal pouch or marsupium within which the eggs are deposited; trochanter with numerous (up to 16) sensory pores on each face; size large (around 16 to 25 mm.). CALLIPAPPINI

bb. Body remaining membranous at maturity; no suggestion of a marsupium of any sort; trochanter with relatively few (four to six) sensory pores on each face; size relatively small (around 4 to 8 mm.)---------- KUWANIINI

INTERMEDIATE FEMALE

(This stage of Callipappini is not known)

a. Globular, protected by a definitely formed test or secretionary covering, usually made up of thin glassy flakes; occurring under or on the ground in sandy localities---------- MARGARODINI

aa. Ovoid or irregularly elliptical, not inclosed within a test, protected only by the irregularities in the bark of the host trees---------- KUWANIINI

LARVA

a. Anterior legs enlarged, stout, fitted for digging, posterior pairs normally stout, rarely lacking; body elongate elliptical to very elongate, sides parallel; no derm disk pores---------- MARGARODINI

aa. Anterior legs not enlarged in relation to other pairs; body elliptical to somewhat elongate elliptical; derm disk pores present, sometimes minute.

b. Second and third antennal segments with several stout lanceolate setae; margins of abdomen with a segmental fringe of relatively elongate, conspicuous setae; claw without denticle, without digitules; beak attached opposite anterior legs---------- CALLIPAPPINI

bb. Antennal segments without stout lanceolate setae; with apical pair of abdominal setae only; claw with denticle, with digitules; beak attached nearly opposite middle legs---------- KUWANIINI

ADULT MALE

a. Anterior legs enlarged, the claw stout, heavily chitinized, the whole obviously fitted for digging, tarsus one-segmented; antennae, where simple, stout. MARGARODINI

aa. Anterior legs not distinctly stouter than others, not specially adapted for digging, tarsus distinctly two-segmented; antennae simple, slender.

b. Antennae with third segment shortest; trochanter with many (about 15) sensory pores on each face, claw without denticle; wings broad, the anal area well developed; apex of penis sheath bilobed; derm disk pores present on abdomen---------- CALLIPAPPINI

bb. Antennae with apical segment shortest; trochanters with relatively few (about four) sensory pores on each face, claw with denticle; wings somewhat narrowed, anal area poorly developed; apex of penis sheath entire; derm disk pores wanting---------- KUWANIINI

TRIBE KUWANIINI HANDLIRSCH

This tribe was established very recently by Handlirsch (*90, p. 1136*) on the basis of the subfamily Kuwaniinae of MacGillivray (*119, p. 76*).

TRIBAL CHARACTERISTICS

Habit.—Living during the growth period in cracks and crevices in the bark of the host; forming a mass of cottony secretion at oviposition.

Adult female.—Body elongate, somewhat broadened posteriorly; derm membranous; antennae with the basal two or three segments definitely enlarged, the basal incompletely chitinized, second segment with one to three sensory pores; legs well developed, trochanters with four to six sensory pores on each face, claw with conspicuous denticle, claw digitules acute at apices, not attaining apex of claw; beak present or wanting, short conical, one-segmented where developed; thoracic spiracles with bar, with pores within atrium, definitely larger than abdominal; abdominal spiracles in four to six well-developed pairs, the anterior pairs the ones present or best developed, each with disk pores within atrium; derm with multilocular disk pores, these usually with rather deeply invaginated centers; derm without spines, disks, or hairs, and with

relatively few setae; anal opening subapical, the tube very poorly developed or wanting; no ventral cicatrices.

Intermediate female.—Body ovoid to irregularly elliptical, more or less chitinized at maturity; antennae reduced to small flat plates bearing one or more stout sensory setae; legs wholly lacking; beak stout conical, one-segmented; thoracic spiracles with or without bar, with pores within atrium, with a few tiny setae on derm close to opening of each; with the four to six anterior pairs of abdominal spiracles developed, with the last two sometimes more or less developed, with disk pores within atrium of all those well developed; derm with simple circular or with multilocular disk pores; without spines, without hairs, setae very few in number; anal opening apical or subapical, the tube small and inconspicuous, or even apparently wanting; ventral cicatrices present or wanting.

Larva.—Body elliptical to rather elongate elliptical; derm membranous; antennae stout, six-segmented, enlarged sensory setae on apical segment only; legs normal, claw with denticle, claw digitules knobbed and surpassing claw apex, or blunted and not attaining claw apex; beak attached opposite middle legs, short conical, one-segmented or indistinctly two-segmented; thoracic spiracles with or without bar, with pores within atrium; abdominal spiracles uncertain; derm pores present, simple or apparently simple, derm without spines or disks, with relatively very few setae, with one or two pairs of apical setae, if the last then one pair smaller.

Adult male.—Based on only one genus, Neosteingelia. See under this below for characteristics.

The known distribution of the genera included here covers the Manchurian subregion of the Palaearctic region and the Alleghenian subregion of the Nearctic region. One species, *Kuwania zeylanica* (Green), that has been assigned here is excluded from consideration in relation to this statement of distribution.

Nothing definite is known regarding the life cycles of the forms included.

The genera assigned to this tribe may be separated as follows:

KEYS TO GENERA OF KUWANIINI

ADULT FEMALE

a. With four (or, rarely, six) pairs of well-developed abdominal spiracles; apex of tibia bearing knobbed digitulelike setae ..... Kuwania
aa. With six well-developed and two poorly developed pairs of abdominal spiracles; tibia without knobbed setae ..... Neosteingelia

INTERMEDIATE FEMALE

a. Thoracic spiracles without bar; ventral cicatrices wanting ..... Kuwania
aa. Thoracic spiracles with bar; ventral cicatrices present ..... Neosteingelia

LARVA

a. Body elliptical; claw digitules knobbed, exceeding claw apex; no ventral cicatrices ..... Kuwania
aa. Body elongate elliptical; claw digitules blunted (perhaps broken), not surpassing tip of claw; a single small, median, posterior, ventral cicatrix ..... Neosteingelia

GENUS KUWANIA COCKERELL

(Pl. 1, D, and figs. 19 and 20)

First established as a zoological unit by Kuwana (*102, p. 44*) in 1902 under the name Sasakia, this genus was later renamed Kuwania by Cockerell (*23, p. 258*), as he had found Sasakia preoccupied. Green (*64, p. 6; 65, p. 425*) has reassigned to this genus another species

originally described as *Monophlebus zeylanicus*, which, while evidently related to Kuwania, is doubtfully congeneric. The material available for study is not adequate for a decision on this point. This species, *zeylanicus*, has been made the type of another genus, Neogreenia, by MacGillivray (*119, p. 78*), but its precise status can not be established until additional specimens are examined. The genus Kuwania has recently been discussed in some detail by Ferris (*51, p. 111*).

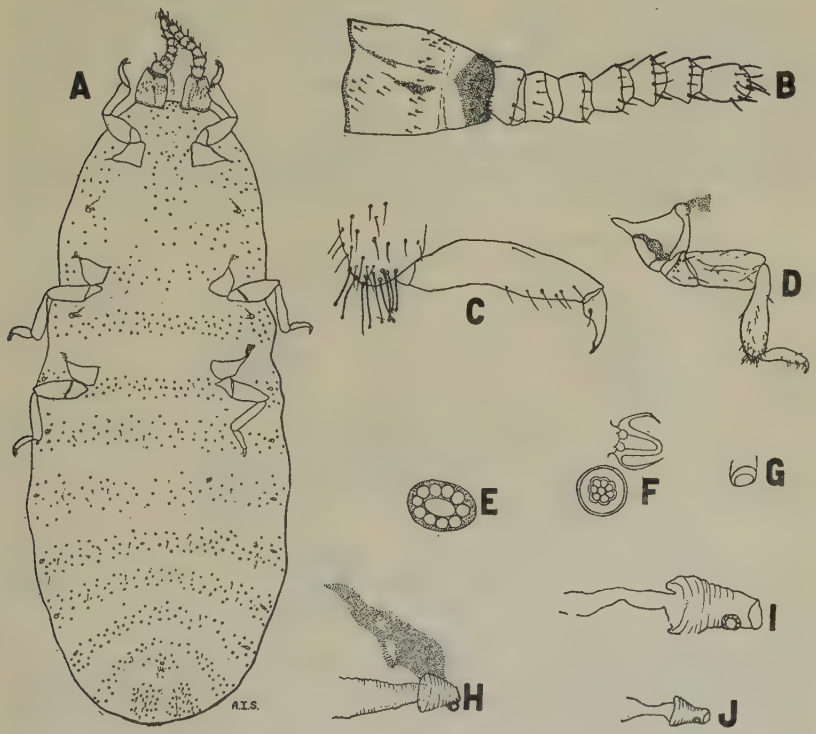

FIG. 19.—*Kuwania quercus*, adult female (specimens collected in 1926): A, outline, ventral, × about 25; B, antenna, × 120; C, apex of tibia, tarsus and claw, × 230; D, leg, × 60; E, spiracular disk pore, × 1,500; F, derm disk pore, surface and section, × 1,500; G, anal tube, × 230; H, thoracic spiracle, × 230; I, abdominal spiracle, × 650; J, same, × 230

GENERIC CHARACTERISTICS

Habit.—As given for the tribe.

Adult female (genotype only).—Body elongate, somewhat broadened toward posterior apex; derm membranous; antennae placed close together on apex of head but without contiguous bases, nine-segmented, the two basal much enlarged, the fifth to eighth each bearing a pair of conspicuously stouter sensory setae, in addition to slender setae, all these on the distal margin of each segment, apical with four such setae, intermediate segments broader at apex than at base, apical ovoid; legs of moderate size, stout, trochanter with four or five sensory pores on each face, all setae small, a number of those on apex of tibia knobbed at apices, resembling digitules, tarsus one-segmented, claw stout, curved, with conspicuous denticle, claw digitules small, slender, acute, hardly extending beyond the middle of the claw; mouth parts usually wanting, sometimes developed; thoracic spiracles of moderate size, opening circular, bar

present, elongate, slender, with one or two disk pores within atrium; abdominal spiracles smaller, with the four to six anterior pairs present,[13] each expanded within opening and each with a single disk pore at inner end of atrium; derm bearing small disk pores of one type only, these nowhere abundant, scattered well over body, more numerous toward posterior apex, each pore with circular, rather deeply invaginated center and an uncertain number, apparently around nine, of poorly developed loculi; body with a few fairly large setae on head and near coxae ventrally, these apparently wanting on abdomen, and with tiny slender setae on both surfaces, these more numerous toward posterior apex of body; no spines or hairs; anal tube subapical, hardly evident, opening a simple ring with very slight internal thickening; no ventral cicatrices.

Intermediate female (genotype only) (preadult).—Very short elliptical, approaching circular in outline; derm somewhat chitinized and minutely and densely areolate; antennae small, circular, somewhat invaginated plates bearing a few, usually three, elongate, slender sensory setae; legs wholly lacking; thoracic spiracles of moderate size, each accompanied by a large circular plate bearing about eight or nine disk pores, with a few disk pores in a wide circle around opening, and with some, usually three, tiny setae behind opening as in the corresponding stage of Margarodes, and some other genera; abdominal spiracles about as large as thoracic, with the four anterior pairs present and each with

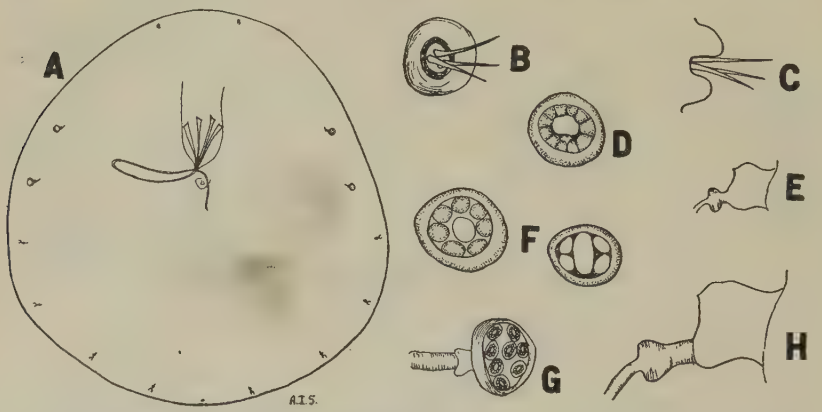

FIG. 20.—*Kuwania quercus*, preadult female: A, outline, × 180; B, antenna, × 650; C, diagrammatic section of same, × 650; D, ventral derm pore, × 1,500; E, abdominal spiracle, × 650; F, dorsal derm pores, × 1,500; G, thoracic spiracle, × 650; H, abdominal spiracle, × 1,500

only about three to five disk pores within, these not arranged on a conspicuous plate; derm bearing a few apparently scattered disk pores, these circular, with circular centers and usually about 10 loculi; derm apparently with a few minute setae in addition to those found near spiracles; anal opening quite small, circular, without chitinized tube; no ventral cicatrices.

Larva (mostly from published information).—More or less uniformly elliptical; derm membranous; antennae placed close together at apex of head, six-segmented, the intermediate segments short, apical longest, somewhat swollen, with four stout, slightly curved sensory setae at apex; legs short and stout, tibia and tarsus apparently fused, claw large, distinctly curved, with distinct denticle and two digitules, these knobbed at apices and exceeding tip of claw; thoracic spiracles each accompanied by a single disk pore; abdominal spiracles uncertain, presumably as in older stages; with a marginal row of small disks on abdominal segments, these apparently simple pores; with a pair of enlarged apical setae, about one-fourth the length of the body, and perhaps with other, minute, setae; anal opening subapical, a simple ring; no ventral cicatrices.

Adult male.—Not known.

[13] Four pairs have been recorded as characteristic for the genus, and that number has been found in specimens of the genotype collected many years ago; specimens collected in 1926, apparently differing in no other respect, show six pairs instead of four.

The genus Kuwania, as here limited, is known only from Japan. If Green's *zeylanica* actually proves congeneric, which is doubtful, the island of Ceylon will be added to the known distribution.

Nothing precise is known regarding the life cycle of the genotype.

Genus Neosteingelia Morrison

(Pl. 1, E, and figs. 21, 22, 23, and 24)

This genus has just been erected by the writer (*136, p. 101*) for the reception of a North American species, *N. texana*, likewise only recently described.

GENERIC CHARACTERISTICS

Habit.—As described above for the tribe.

Adult female.—Decidedly elongate, somewhat broader toward posterior apex; derm wholly membranous; antennae well developed, placed close together at anterior apex of body, but the bases not contiguous, nine-segmented, the basal much enlarged, not entirely chitinized, second very short, with a single sensory pore, remainder increasingly longer toward apex, and those beyond third increasingly, although not strongly, moniliform, segments 4 to 7 each with a single enlarged marginal sensory seta, eighth segment with two of these, ninth segment with four to six of such setae on the almost truncate apex, apical two or three segments faintly and irregularly imbricated; legs well developed, of moderate size, rather stout, each trochanter with very few setae, these minute, tibial and tarsal setae larger, but still small, slender, not numerous, tarsus faintly imbricate-reticulate, claw stout at base, curved, with prominent subapical denticle on inner face, claw digitules short, acute, barely surpassing middle of claw; beak present, small, moderately conical, with no more than a single definite segment, with several acute, apical, sensory setae; thoracic spiracles of moderate size, each with narrow bar with broadened inner end and a cluster of multilocular disk pores within atrium; abdominal spiracles opening submarginally and ventrally, the six anterior pairs each well developed and evident, although plainly smaller than the thoracic, each with distinct atrium containing one or more multilocular disk pores, the two posterior pairs reduced to much smaller slitlike openings, doubtfully functional, the apical distinctly separated from the anal opening; derm pores of only one type, small, multilocular disk, with large, apparently simple, invaginated, circular center and numerous (around 14) loculi, these distributed over the body in indefinite segmental arrangement, somewhat more abundant at the posterior apex, nowhere numerous; derm with small inconspicuous setae set in large, flat, circular bases, these likewise more numerous toward the posterior apex of the body; anal opening subapical, anal tube very short, made up mostly of a small, flattened, chitinized area with a few areolations, possibly representing degenerate polygonal wax pores, in its middle; no ventral cicatrices.

Intermediate female.—An ovate sac, more or less strongly narrowed anteriorly, nowhere heavily chitinized, but densely irregularly alveolate over whole surface; antennae reduced to small oval disks bearing three or four sensory setae; legs wholly lacking; beak small, short conical, not more than one-segmented, with a few (perhaps four) sensory setae at apex; thoracic spiracles of moderate size, each with narrow bar, a circular cluster of multilocular disk pores within atrium, and two or three tiny setae on derm behind opening; abdominal spiracles somewhat smaller, the six anterior pairs, as in adult, well developed, each with one or more disk pores within atrium, the two remaining pairs tiny simple tubes; spiracular pores of a single type, multilocular disk with usually bilocular center and numerous (around nine) loculi; derm pores of one type, as far as can be determined not multilocular, with a large, open, circular center, the whole pore somewhat invaginated, these pores distributed over the body but nowhere numerous or crowded; body with very small setae scattered sparsely; no spines or hairs; anal tube distinctly dorsal in position, small, consisting of a transverse chitinized area with an anteriorly incompletely chitinized ring, the opening thus formed apparently closed by a chitinized flap hinged to the incomplete portion of the

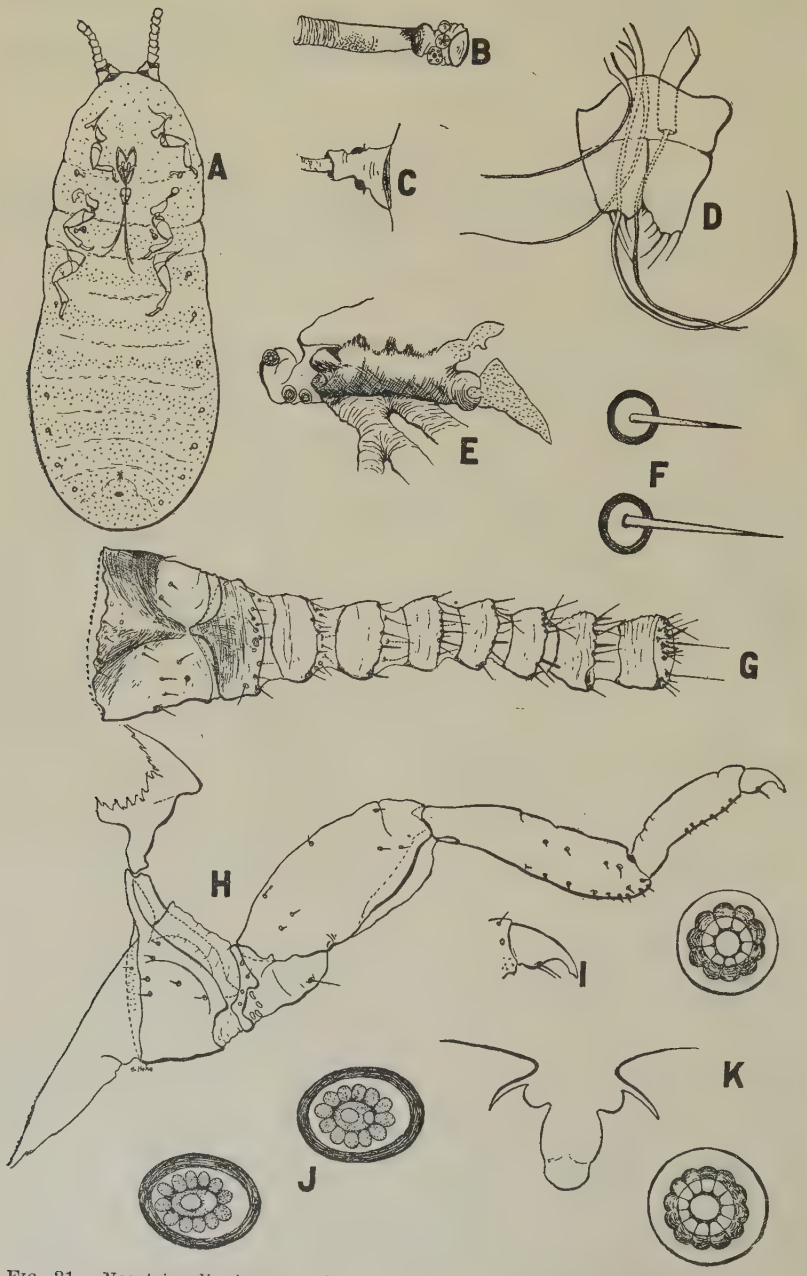

FIG. 21.—*Neosteingclia texana*, adult female: A, outline of body, ventral, × 12; B, abdominal spiracle, × 230; C, same, in section, × 230; D, beak, × 115; E, thoracic spiracle, × 230; F, derm setae, × 1,500; G, antenna, × 120; H, leg, × 120; I, tarsal claw, × 230; J, disk pores adjacent to thoracic spiracles, × 1,500; K, derm disk pores, surface and sectional views, × 1,500

ring, this arrangement practically identical with the corresponding stage of Margarodes; ventral cicatrices present, small, circular, in two submarginal rows of five, one on each side of the posterior portion of the abdomen.

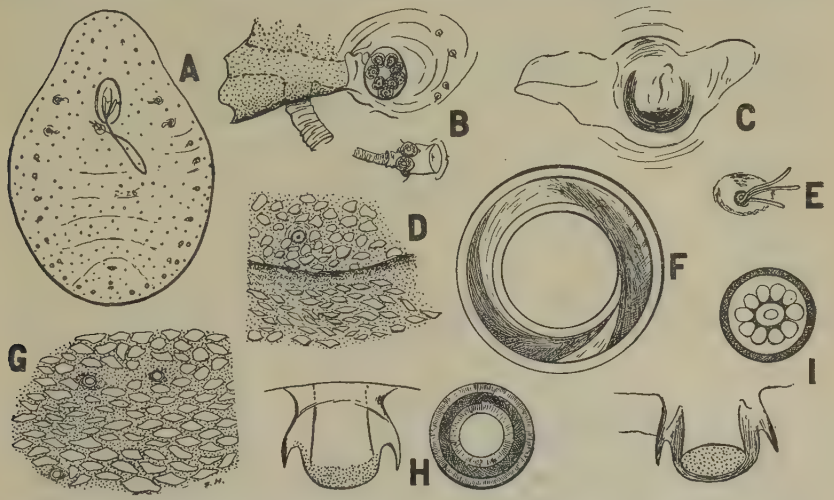

FIG. 22.—*Neosteingelia texana*, intermediate female: A, outline of body, × 20; B, thoracic (above) and abdominal (below) spiracles, × 230; C, anal opening, × 530; D, portion of derm showing areolate condition, × 230; E, antenna, × 230; F, cicatrix, × 1,500; G, another portion of derm, × 230; H, simple circular pore, surface and section, × 1,500; I, spiracular multilocular disk pore, surface and section, × 1,500

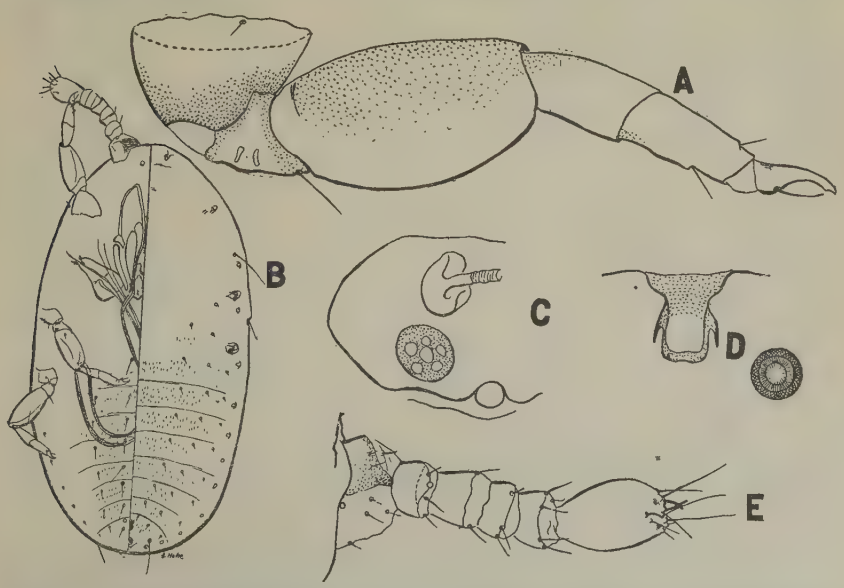

FIG. 23.—*Neosteingelia texana*, larva: A, leg, × 650; B, outline of body, dorsal and ventral, × 115; C, thoracic spiracular region, × 1,500; D, marginal disk pore, surface and section, × 1,500; E, antenna, × 330

Larva.—Body elongate elliptical, sides nearly parallel through the middle section; derm membranous; antennae six-segmented, stout, second segment with a single sensory pore, apical largest, somewhat swollen, bearing three sensory setae and an invaginated forked organ at apex; legs small, rather

stout, trochanter with two pairs of sensory pores, claw somewhat curved, with distinct denticle, claw digitules blunted but not knobbed at tips, barely attaining the denticle; beak moderately elongate conical, distinctly two-segmented, the apex with two acute sensory setae; thoracic spiracles of moderate size, each with bar and with a multilocular disk pore within atrium; abdominal spiracles extremely minute, number not certainly determined, appearing as very delicate tubes, without pores in atrium; margin of body with a segmental row of apparently simple disk pores, of the type described for the intermediate stage but much smaller, these totaling 13 pairs; derm with a

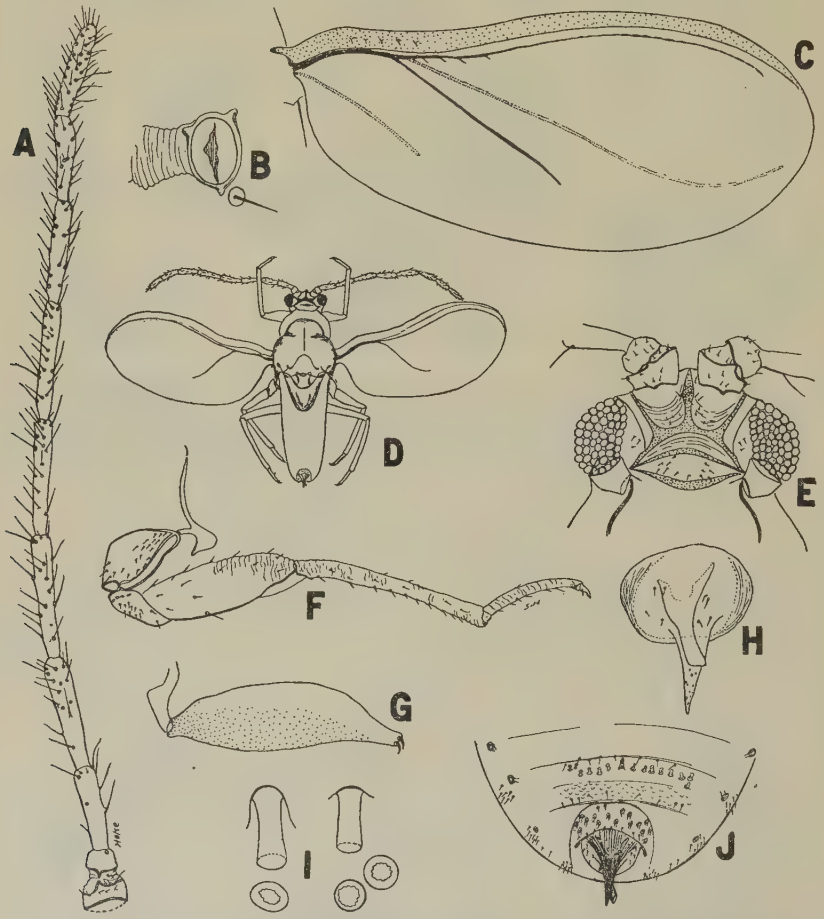

FIG. 24.—*Neosteingelia texana*, adult male: A, antenna, × 60; B, abdominal spiracle, × 530; C, wing, × 30; D, outline, × 12; E, head, × 60; F, leg, × 60; G, halter, × 120; H, penis sheath, ventral, × 120; I, tubular pores from apex of abdomen, × 530; J, apex of abdomen, × 50

few tiny setae, mostly near pores; apex of abdomen with one apical pair of larger setae and one subapical pair somewhat smaller, these both small and inconspicuous; anal opening subapical, with a small conical chitinized tube attached; with a single small, circular, median, posterior, ventral cicatrix.

Adult male.—Of the usual elongate shape; apex of head short triangular, antennal segments beyond second elongate, slender, cylindrical to slightly clavate, irregularly nodulose, bearing short, inconspicuous setae indefinitely arranged, the segments successively shorter to apical; legs elongate, slender, trochanter with several (about four) sensory pores on each face, a very few

small setae on femur, under sides of tibia and tarsus with definite rows of small but stiff setae, tarsus distinctly two-segmented, claw slender, only slightly curved, with subapical denticle, claw digitules slender, not knobbed, not even attaining claw denticle; wing faintly clouded, the costal complex continued as a narrowing band to the wing apex, basal diagonal vein, although faint, elongate, extending beyond middle of line from its base to wing margin, diagonal light streaks very faint, but present; halteres widened, the apex with one or, rarely, two short, stout, acutely pointed, curved setae; abdomen membranous, except for faintly chitinized transverse segmental plates, near posterior apex dorsally with two transverse clusters of tubular ducts; without even a suggestion of apical or lateral fleshy tassels; with six observed pairs of abdominal spiracles, the two posterior pairs not located, each of these a simple ring; penis sheath much enlarged at base, the tapering tip protruding from the base as if from the center of a plate, the lower valve somewhat curved downward and expanded at tip; without disk derm pores; with a few slender setae on membranous portions of body.

This genus includes a single species, *texana*, known from the Alleghenian subregion of the Nearctic region. Nothing definite regarding the life history of the species is available.

TRIBE MARGARODINI COCKERELL

This tribe appears to have been first established by Cockerell (*17, p. 275*) in 1899 for the reception of the genus Margarodes. As here used its status is almost identical with the original, since only one other genus, closely related to Margarodes, has been added.

Tribal Characteristics

Habit.—Inclosed during the growth period in a heavy test or a thin but very hard test; living on the roots or stems of plants growing in sandy localities.

Adult female.—Body stout elliptical to almost circular; derm not chitinized; antennae fairly well to well developed, six-segmented to eight-segmented, rarely apparently 14-segmented to 16-segmented, second antennal segment with a single sensory pore; anterior legs much enlarged, very stout, the claw large and heavily chitinized, obviously fitted for digging; posterior pairs stout and usually with relatively large claw, but not conspicuously enlarged, trochanter with around five sensory pores on each face, claw without denticle, claw digitules acute at tips, not attaining apex of claw; beak wanting; thoracic spiracles with bar, this sometimes only weakly developed, with or without pores within atrium, definitely larger than abdominal; abdominal spiracles present, in from six to eight pairs, if less than eight pairs then the posterior lacking, very rarely (one species) apparently and possibly actually lacking, with or without pores within atrium; derm disk pores present, mostly multilocular, showing decided variation in details of organization; derm with or without stout spines, without disks, with or without hairs, setae present, usually numerous, these, with the hairs, often giving the body a densely hirsute appearance; anal opening apical or subapical, tube small or not developed; no ventral cicatrices.

Intermediate female.—Approximately globular; inclosed within a protective test; derm membranous; antennae reduced to flat plates, sometimes invaginated, bearing one or more sensory setae; legs wanting; beak stout conical, one-segmented; thoracic spiracles without bar, with pores within atrium, with a few tiny setae on derm near opening; abdominal spiracles in six to eight pairs, if less than eight, then the posterior ones lacking, with or without pores within atrium; derm pores rarely present, mostly lacking; spines, hairs, and setae other than those near spiracles lacking; anal opening apical, tube practically nonexistent; with a few small, circular, ventral cicatrices in definite arrangement on the abdomen.

Larva.—Body elongate elliptical to very elongate, parallel-sided; derm membranous; antennae stout to moderately slender, two-segmented to six-segmented, apical segment only bearing sensory setae; anterior legs much enlarged, stout, fitted for digging, remaining pairs normally developed, rarely lacking, claw without denticle, claw digitules acute; beak attached opposite fore or middle legs, small, short conical, one-segmented; thoracic spiracles without

derm pores, with disk pores within atrium; abdominal spiracles uncertain as to number with many species, mostly without disk pores within atrium; without derm disk pores; with a single or with two unequal pairs of apical setae; anal opening apical or subapical, the tube not or hardly developed; with a single, small, circular, median, ventral cicatrix.

Adult male.—Rather stouter than with other groups; antennae simple or pectinate, 7-segmented to 10-segmented or perhaps to 13-segmented, mostly stout, the third segment shortest where simple; legs without bifurcate setae, trochanter with several (around 12) sensory pores on each face, tarsus one-segmented, claw without denticle, claw digitules acute, not attaining claw apex; wings broad, the basal diagonal elongate, costal complex truncate, apical diagonal wanting or more or less developed; halteres broad, or at least somewhat broadened, with a single short, stout, apical seta on each; derm of abdomen bearing large, transverse, definitely chitinized plates; with one or two clusters of elongate tubular pores near apex of abdomen dorsally; penis sheath stout, entire at apex, the lower valve short, straight, or somewhat curved downward; derm disk pores wanting on abdomen.

The known representatives of this tribe are very widely distributed, having been found in one or more subregions of the Palaearctic, Ethiopian, Oriental, Neotropical, and Nearctic regions.

Little precise information is available regarding the life histories of the included species.[14]

Two genera are recognized here. Almost certainly others will be erected when the different stages and the habits of some of the species now assigned to Margarodes are better known. The included genera may be separated by the following keys:

KEYS TO GENERA OF MARGARODINI

ADULT FEMALE

a. Claw of anterior leg, while large, elongated, mostly tapering nearly uniformly from base to tip, without a definitely formed heel even where base is expanded; derm very frequently with heavy spines; antennae normally at least seven-segmented, elongated, tapering gradually. ..... Margarodes

aa. Claw of anterior leg very stout, wider than long, with a prominent heel; derm without heavy spines; antennae normally six-segmented, short, tapering strongly from base to tip ..... Neomargarodes

INTERMEDIATE FEMALE

There is no certain basis known for separating this stage of the two genera.

LARVA

a. Body very elongate, parallel-sided; beak attached opposite middle coxae; apical antennal segment typically stout ..... Margarodes

aa. Body elongate elliptical or elongate ovoid only; beak attached nearer fore than middle coxae; apical antennal segment slender ..... Neomargarodes

ADULT MALE

a. Antennae entire ..... Margarodes

aa. Antennae conspicuously pectinate ..... Neomargarodes

GENUS MARGARODES GUILDING

(Pls. 1, F, and 2, A, and figs. 25, 26, and 27)

This genus, erected by Guilding (*83, p. 115*) in 1829, in an interesting and relatively detailed paper, is the oldest one that is con-

[14] See Marchal (*120*) for a recent review of the known information and for original observations in this field.

sidered in the present discussion, although the genotype, *formicarum*, is by no means the oldest known species, at least one, *polonicus*, which was described by Linnaeus, having been known for many years before 1829. The genus Porphyrophora was established by Brandt (*4, p. 355*) in 1833 shortly after the erection of Margarodes and for many years was in current usage for the reception of the European species of the genus. Sphaeraspis was indicated by Giard (*63, p. 684*) in 1897 as a subgenus of Margarodes, but is not accepted as valid at the present time. A total of 10 supposedly valid species had been described up to the time of the publication of the Fernald

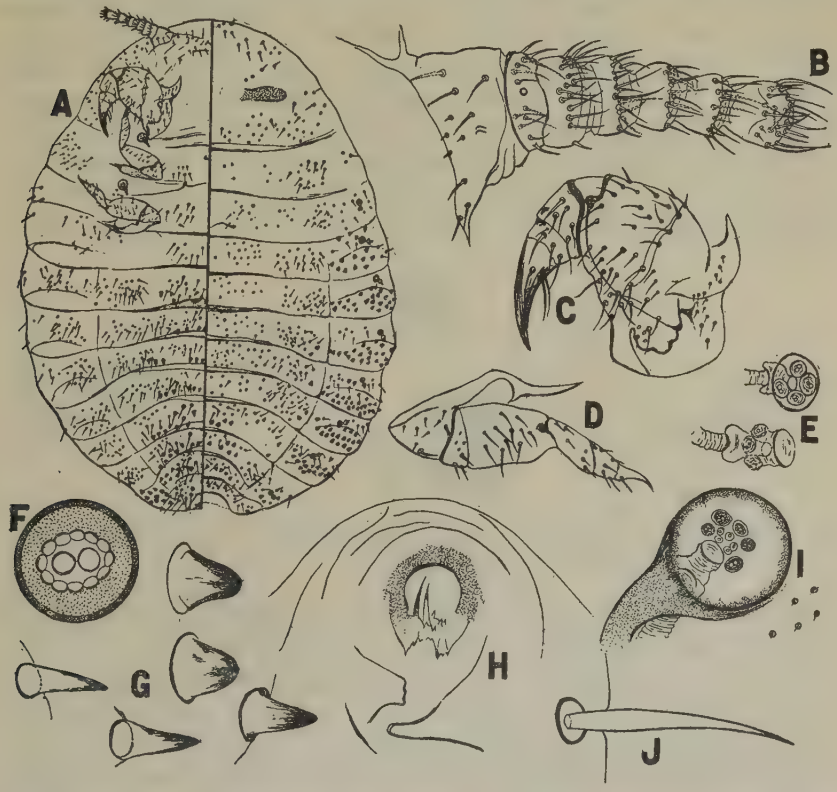

FIG. 25.—*Margarodes meridionalis*, adult female: A, outline, dorsal and ventral, × 80; B, antenna, × 120; C, anterior leg, × 60; D, posterior leg, × 60; E, abdominal spiracle, two views, × 230; F, multilocular disk pore, × 1,500; G, derm spines, × 530; H, anal opening, × 650; I, thoracic spiracle, × 230; J, derm seta, × 530

Catalogue of the Coccidae in 1903 (*46*). Two of these have been subsequently indicated for synonymy, and the total list of supposedly valid species has been increased to 20, largely through the activities of Green and Brain.

GENERIC CHARACTERISTICS

Habit.—Living during period of growth, and probably for most or all of remainder of life, in sandy soil, feeding on plant roots; immature stages forming a thin but very firm glassy secreted test.

Adult female.—Very broadly elliptical to nearly circular in outline as mounted, size varying greatly within the species; derm membranous; antennae

normally seven-segmented to eight-segmented to apparently 14-segmented to 16-segmented, stout, broadest at base, tapering somewhat, intermediate segments wider than long, often stout moniliform, apical segment bearing several stout sensory setae, intermediate segments often with such setae also, these sometimes quite numerous, second segment with a single sensory pore; legs much modified, the anterior pair strongly enlarged, trochanter and coxa fused, trochanter with numerous (five or more) sensory pores on each face, tarsus and claw often fused, joint between tibia and tarsus not flexible, claw very greatly enlarged, very heavily chitinized, claw digitules apparently represented by setae, sometimes in two pairs, sometimes one pair, these sometimes much enlarged, flattened toward bases, middle and hind legs smaller, but also stout, usually resembling the anterior pair, the claw more slender; beak apparently always wanting; interior framework of mouth parts not observed, derm between anterior legs sometimes showing wrinkling or folding at the point usually bearing the beak; thoracic spiracles of moderate size, with circular opening, more or less developed bar, and small internal disk pore band or cluster; abdominal spiracles distinctly smaller, tubular, with disk pore collar within atrium of each, the number present, so far as can be determined, varying from six to eight pairs, apparently entirely lacking in one species, only the two anterior reported present in another, the reduction from the maximum number apparently occurring from the posterior apex; derm pores of one type only, multilocular disk, but exhibiting some variation in details, some with from three to six large central loculi surrounded by a circle of smaller loculi, this sometimes double, some with bilocular center surrounded by smaller loculi,

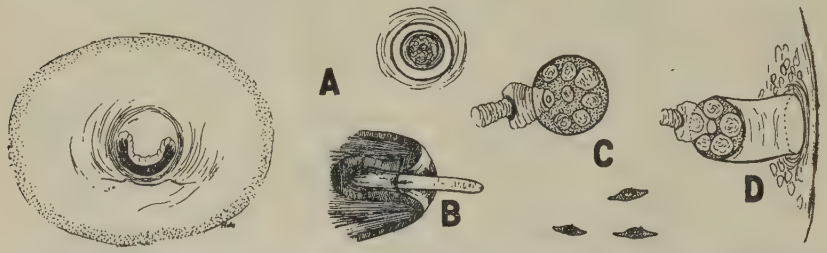

FIG. 26.—*Margarodes meridionalis*, intermediate female: A, anal opening, with adjacent cicatrix, × 530; B, antenna, × 530; C, thoracic spiracle and adjacent setae, × 530; D, abdominal spiracle, × 530

some with several (around five) large central loculi, but lacking the chain of small loculi; derm in some species bearing stout spines, usually in conspicuous bands or clusters, these sometimes lacking, in this case the body with numerous, long, hairlike setae only; derm with or apparently without stout hairs, or, perhaps more correctly, hairlike spines, with slender setae, these more or less abundant, the body, in general, abundantly provided with setae or with setae, spines, and hairs; anal opening apical to subapical, the opening typically a narrow semicircular slit, with a more or less developed, small, short, internal tube.

Intermediate female (preadult).—Body inclosed within a globular or irregular, usually hard, shining test, presumably composed of secreted matter and usually in the form of overlapping, scalelike, thin layers; body itself approximately globular; the derm membranous, but usually faintly but densely alveolate; antennae represented by two tiny disks bearing one or more sensory and other setae; legs wholly lacking; beak small, inconspicuous, apparently one-segmented; thoracic spiracles of moderate size, tubular, without bar, atrium with a circular cluster of disk pores or with a circular wax-producing plate, each spiracle with one to several minute setae immediately behind the opening on the surface of the derm; the abdominal spiracles varying decidedly, some species with some, at least, minute, in uncertain numbers, often with the first two pairs larger than the remainder, each spiracle typically with internal disk pore or pores as in thoracic, but without minute setae adjacent to the opening, first pair usually, and perhaps always, set much farther away from the median line than the remainder, with seven to eight or perhaps six to eight pairs, actual number present uncertain in one species examined; loculate derm disk pores wanting or present (in one species examined only) as clusters of

large circular pores with round center and about nine large loculi surrounding each thoracic spiracle; derm without setae, except those mentioned in connection with the thoracic spiracles; anal opening a semicircular or even longer slit, with or without a short internal tube attached; ventral cicatrices represented by a few small circular disks, the number and arrangement varying, perhaps, with the species. (Earlier stages resembling the preadult except for smaller size and some other slight modifications.)

Larva.—Body very elongate, slender; derm membranous; antennae typically two-segmented to four-segmented, stout, the apical one or two segments enlarged, stout oval, one species included here for the present with six-segmented

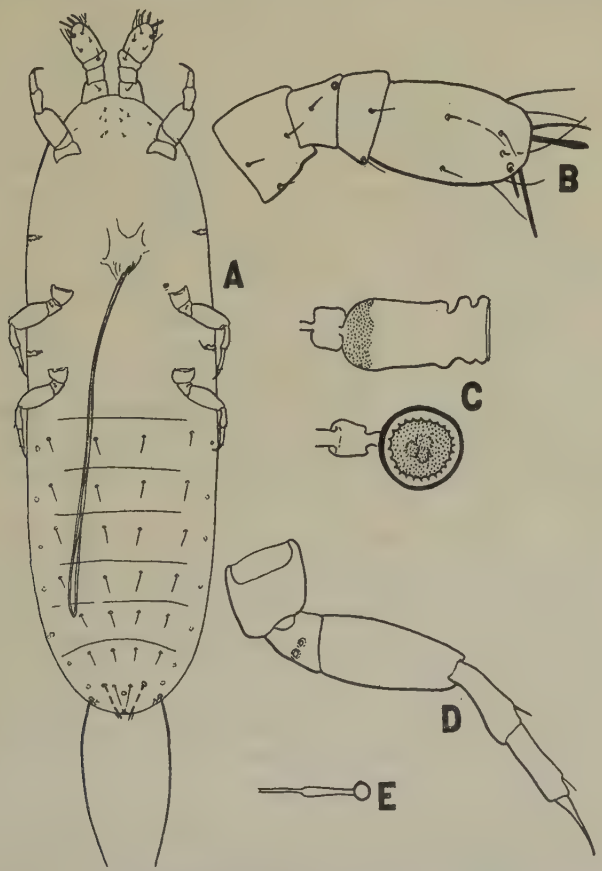

FIG. 27.—*Margarodes formicarum,* larva: A, outline, ventral, × 115; B, antenna, × 460; C, thoracic spiracle, × 1,500; D, leg, × 460; E, abdominal spiracle, × 1,500

antennae with the terminal segment elongate and slender, in any case the apical segment with one or more stout, often distinctly clavate, sensory setae; legs mostly short and stout, the anterior pair distinctly larger than the other two, the middle and hind pairs sometimes lacking, definite fusing of some parts, as trochanter and femur, or tibia and tarsus, sometimes evident in the anterior pair of legs, claw elongate, nearly straight, claw digitules tapering setae, not even approximating the claw tip; beak small, poorly developed, attached opposite middle coxae, framework of mouth parts situated well behind the anterior pair of legs; thoracic spiracles of moderate size, with a disk pore or pore plate within atrium of each; abdominal spiracles present, much smaller, with or without disk pore, number uncertain, probably identical with that in

other stages; derm without disk pores; with one or two unequal pairs of enlarged apical setae and, at least sometimes, with additional small or inconspicuous setae scattered over the body; anal opening apical, with a small, not heavily chitinized, internal tube attached; with a single, very small, median, subapical, ventral cicatrix usually present.

Adult male.—Elongate, but stouter than in other genera examined, the abdomen tending to be broadened, at least in mounted specimens; antennae in all specimens examined 10-segmented, segments short and stout, more or less clavate, not nodose or nodulose, bearing many small setae, antennal segments variously reported as from 9 to 13, the length of the segments gradually increasing from base to apex, the terminal longest; compound eyes large, the facets large, the eyes approaching or contiguous below, the outline elongate dorso-ventrally, not circular as viewed from the side; legs stout, the parts of each enlarged, the fore pair more strongly modified than the others, tarsus and claw very stout, heavily chitinized, tarsus in all legs distinctly one-segmented, trochanter bearing numerous sensory pores, middle and hind claws simple or conspicuously trifurcate, claw digitules short, stout, acute-tipped setae, setae on leg parts small, except in some species, here, in part, enlarged and flattened at bases on tibia and tarsus; wings rather broad, faintly clouded, venation not altogether certain, sometimes with an apical diagonal vein as in Xylococcus, the other veins about as usual, but shifted somewhat in position; halteres slender to broad, with a single short, stout, acute, apical seta, fitting into a circular socket in the wing lobe; abdomen membranous laterally and ventrally, but bearing dorsally a segmental series of large, transverse, almost contiguous, chitinized plates, sometimes with a similar series on each margin, these circular or quadrate; abdomen without any suggestion of apical or lateral marginal fleshy tassels; dorsally with a single, approximately circular, or two transverse clusters of tubular ducts producing glassy threads; penis sheath broad at base, stout, sometimes expanded basally, conical to very stout conical, entire or cleft at apex, ventral valve elongate, nearly attaining or exceeding the tip of the penis sheath, apex rounded or blunted; with fleshy penis of undetermined structure; derm normally without loculate disk pores of any sort, with tiny simple "pores" in clusters on abdominal segments; derm setae small, inconspicuous, mostly in rows or small clusters.

The known distribution of this genus, as here accepted, is very wide, covering the European and Mediterranean subregions of the Palaearctic region, the South African subregion of the Ethiopian region, the Indian subregion of the Oriental region, the Chilean and Antillean subregions of the Neotropical region, the Rocky Mountain and Alleghenian subregions of the Nearctic region, and, finally, the Galapagos Islands. The habit of the insects is such that discovery is often more or less accidental, and it seems very probable that many additional species will be found in suitable situations in numerous new localities throughout the world.

Although the literature on this genus is comparatively extensive and includes frequent references to the peculiar habits of its species, no precise statement regarding the length of the normal life cycle appears to have been made. The species live in sandy locations, usually subject to definite periods of drought, and they have, presumably in consequence, developed a most remarkable physiological adaptation, in that they can, while in the immature stages, remain alive for years. The published record for retention of vitality is 17 years (*130, p. 228; 50, p. 27*). Another and, if correctly interpreted, presumably unique characteristic of these insects is the existence of definite true prepupal and pupal stages in the females of the included species. The latest discussions of this condition are those of Brain (*3, p. 182*) and Marchal (*120*), but it was reported by earlier writers. If it actually exists, a parallel situation may be found in some of the other forms having much modified intermediate female stages.

The classificatory treatment which it has been possible to accord here to the genus Margarodes is very unsatisfactory. Almost certainly it will be necessary to erect additional genera to care for some of the more widely divergent species now included in the genus. One example of this is to be found in *M. hirsutissimus* Hall, which, in every available stage, shows one or more characters strongly diverging from the typical condition as exemplified by the genotype. Thus, the larva has six-segmented antennae, with the apical segment elongate and slender in contrast to the four or fewer stout segments of typical Margarodes; the intermediate form has large clusters of disk pores around the thoracic spiracles, not present in other forms examined, and the adult female apparently lacks the abdominal spiracles and apparently possesses multiarticulate antennae. Again, from published illustrations there appear to be two distinct types of development in the male intromittent organ, while the number of adult male antennal segments has been reported as ranging from 9 to 13. There are so many important gaps in the available study material, and stages supplementary to the adult female are so frequently lacking, that it is considered inadvisable to attempt to formalize these differences at this time by the erection of new generic names.

More than 20 species have been associated with this genus. Adult females believed to represent 10 of these, although only rarely actually type or cotype specimens, have been examined. Some European synonymy, suggested by Lindinger (*113, p. 372*), is not verifiable. The species assigned here are *brasiliensis* Wille (*174, p. 83*) from Brazil, *buxtoni* Newstead (*151, p. 10*) from Algeria, *capensis* Giard (*63, p. 683*) from South Africa, *formicarum* Guilding (*83, p. 115*) from the Lesser Antilles, *greeni* Brain (*3, p. 187*) from South Africa, *gallicus* (Sign.) (*158, p. 380*) (=*polonicus* according to Lindinger), *hamelii* (Brandt) (*4, p. 355*) from Armenia, *hiemalis* Cockerell (*19, p. 416*) from New Mexico, *hirsutissimus* Hall (*84, p. 1*) from Egypt, *indicus* Green (*67, p. 69*) from India, *mediterraneus* Silvestri (*159, p. 140*) from Italy, *meridionalis* Morrison (*136, p. 102*) from Georgia and Florida, *newsteadi* Brain (*3, p. 187*) from South Africa, *niger* Green (here placed in Neomargarodes), *papillosus* Green (*67, p. 74*) from India, *parieli* Vayssière (*167, p. 258*) from Morocco, *peringueyi* Brain (*3, p. 188*) from South Africa, *perrisii* (Signoret) (*158, p. 381*) (=*polonicus* according to Lindinger), *polonicus* (Linnaeus) (*115, p. 456*) from Europe, *rileyi* Giard (*63, p. 683*) from Florida and the Bahamas, *ruber* Brain (*3, p. 189*) from South Africa, *similis* Morrison (*134, p. 143*) from the Galapagos Islands, *trimeni* Giard (*63, p. 684*) from South Africa, and *vitium* Giard (*60, p. 126; 61, p. 412; 62, p. 710*) from Chile and Argentina.

The following attempt to separate the adult females that have been examined is not based on an extended critical comparative study of the specimens, and at best can be regarded as no more than suggestive.

KEY TO AVAILABLE ADULT FEMALES OF MARGARODES

a Without traces of stout spines on any part of the body.

b. Posterior apex of body produced to form a conspicuous, stout conical boss bearing long setae directed diagonally anteriorly; six pairs of abdominal spiracles----------*hiemalis* Cockerell

bb. Posterior apex of body uniformly rounded, no trace of protuberance.
c. Antennae eight-segmented; reported as with only the two anterior pairs of abdominal spiracles developed.
buxtoni Newstead[15]
cc. Antennae apparently 14-segmented to 16-segmented; apparently entirely without abdominal spiracles (probably present but minute)——*hirsutissimus* Hall
aa. With some stout spines on the body, these often numerous, in loose transverse dorsal and marginal bands.
d. Body spines, particularly those of the abdominal region, distinctly enlarged and flattened at apices; disk pores in atrium of abdominal spiracles numerous (around 10 to 16) and accompanied by tiny tubular ducts——*vitium* Giard
dd. Body spines all more or less conical with the apices rounded or tapering to points; abdominal spiracular disk pores much fewer (with at most about five or six), and atrium without the tiny tubular ducts.
e. Normal type of derm pore oval, with bilocular center surrounded by a simple row of loculi.
f. No spine clusters along body margin anterior to first pair of abdominal spiracles——*meridionalis* Morrison
ff. At least one spine cluster at body margin anterior to first pair of abdominal spiracles——*papillosus* Green
ee. Normal type of derm pore approximately circular, with multilocular center (four or more) and numerous loculi around the center.
g. Thoracic spiracles with as many as 14 to 17 multilocular disk pores with bilocular centers within atrium of each——*formicarum* Guilding
gg. Thoracic spiracles with, at most, as many as eight, and usually with from two to four, multilocular disk pores within the atrium of each.
h. Posterior abdominal spines, at least, quite stout, strongly constricted apically and normally with a small but distinct apical nipple; thoracic spiracles usually with six to eight multilocular disk pores within atrium——*rileyi* Giard
hh. None of the body spines normally showing an apical nipple, these instead usually bluntly rounded or pointed at apices.
i. Opening of thoracic spiracles each normally with a small, but distinct, almost spinelike seta at edge in addition to two of the usual minute setae——*similis* Morrison
ii. Opening of thoracic spiracles each without such a small spinelike seta.
j. Atrium of each thoracic spiracle usually with two, sometimes with three, multilocular disk pores, opening of each normally with four minute setae adjacent——*capensis* Giard
jj. Atrium of each thoracic spiracle usually with five to seven multilocular disk pores; opening of each normally with two minute setae adjacent.
trimeni Giard

Genus Neomargarodes Green

(Pl. 2, B, C, and figs. 28, 29, and 30)

This genus was established by Green (*70, p. 263*) in 1914 for a remarkable male coccid from the Sahara Desert. Marchal (*120, p.*

[15] Included from literature only, no specimens examined; from the literature *gallicus* and *perrisii* of Signoret (=*polonicus* Linnaeus according to Lindinger) certainly, and *parieli* Vayssière very probably, belong in close association with Hall's *hirsutissimus*.

1092) subsequently described a new species, *N. trabuti*, with a characterization of female and other stages in addition to the adult male, and one of the species, *niger*, described as Margarodes by Green, is now added to the genus.

GENERIC CHARACTERISTICS

Habit.—Living during the growth period within a globular, thick-walled, secreted test.

Adult female.—As mounted, very broad oval to almost exactly circular; derm membranous; antennae six-segmented, short and stout, broad at base, the apical

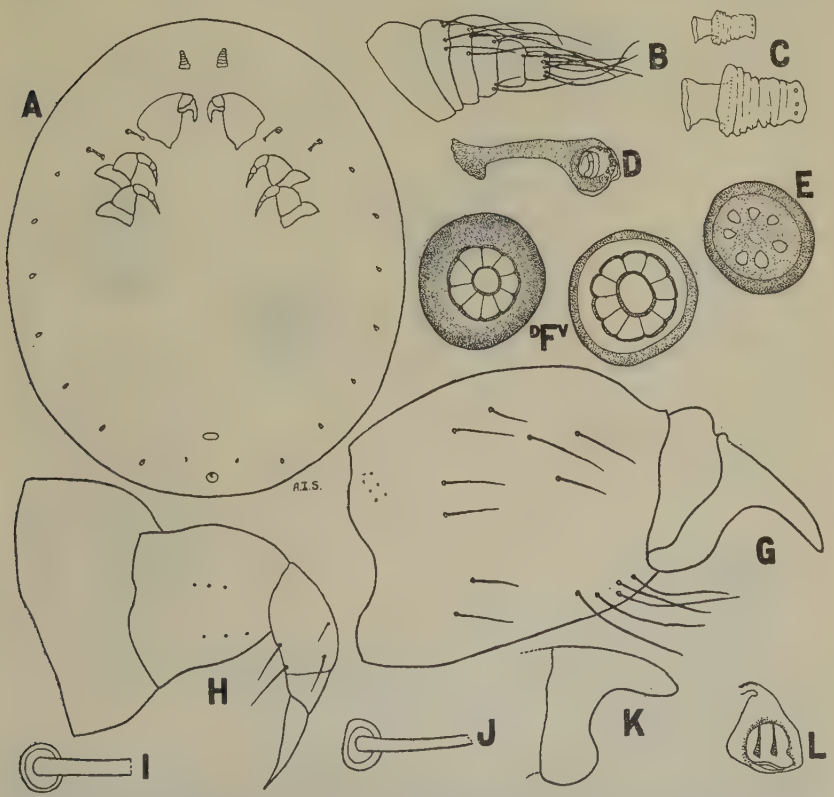

FIG. 28.—*Neomargarodes trabuti* (except E and K), adult female: A, outline, optical section, × 7.5; B, antenna, × 60; C, abdominal spiracle, above × 60, below × 120; D, thoracic spiracle, × 60; E, disk pore within atrium of abdominal spiracle of *N. niger*, × 1,500; F, multilocular derm disk pore, (D) dorsal and (V) ventral, × 1,500; G, portion of anterior leg, × 60; H, posterior leg, × 60; I, base of ventral, long, slender, body seta, × 650; J, base of dorsal, long, slender, body seta, × 650; K, claw of anterior leg of *N. niger*, × 60; L, anal tube, × 60

segment slender, the segments nearly cylindrical; anterior legs much enlarged, as in Margarodes, the parts more or less fused but with very different claw, this, instead of elongate and nearly uniformly tapering, very broad at base and with distinct "heel," the width greater than the length of the short, protruding claw proper, posterior pairs of legs as in Margarodes; no traces of mouth parts observed; thoracic spiracles of moderate size, with narrow bar and row of disk pores at opening; abdominal somewhat smaller, with the posterior smallest, in eight pairs, each, except the apical at times, with one to several small disk pores just within opening; derm pores of a single type, multilocular disk, nearly circular, with circular to somewhat oval centers and about seven to eight, or occasionally more, loculi; derm without spines, apparently without hairs, but

with numerous long, slender, hairlike setae, giving the body an appearance as if clothed with hair; anal opening approximately apical, semicircular, with a small, somewhat chitinized tube attached; no ventral cicatrices.

Intermediate female (preadult).—Approaching a globular form; derm becoming more or less heavily chitizined at maturity; antennae reduced to tiny flat plates or cones bearing one or more small setae; legs wholly lacking; beak small, poorly formed, internal framework moderately developed; thoracic spiracles of moderate size, without bar, with a circle of disk pores internally and with several, usually four to six, tiny setae behind the opening of each; abdominal spiracles somewhat to considerably smaller, with eight pairs, each with internal disk pores accompanying it; no derm pores (see under ventral cicatrices); no body setae observed other than those adjacent to spiracles; anal opening apical, structure not certain, apparently very simple; ventral cicatrices relatively numerous, small to very small, circular, in two or more divergent rows on the under side of the abdomen.

Larva (one species only).—Elongate, somewhat broader through the abdominal region, but not elongate in the sense of typical Margarodes; derm membranous, antennae stout, six-segmented, the apical somewhat enlarged, diagonally truncate at apex, bearing several short, stout, sensory setae; anterior legs

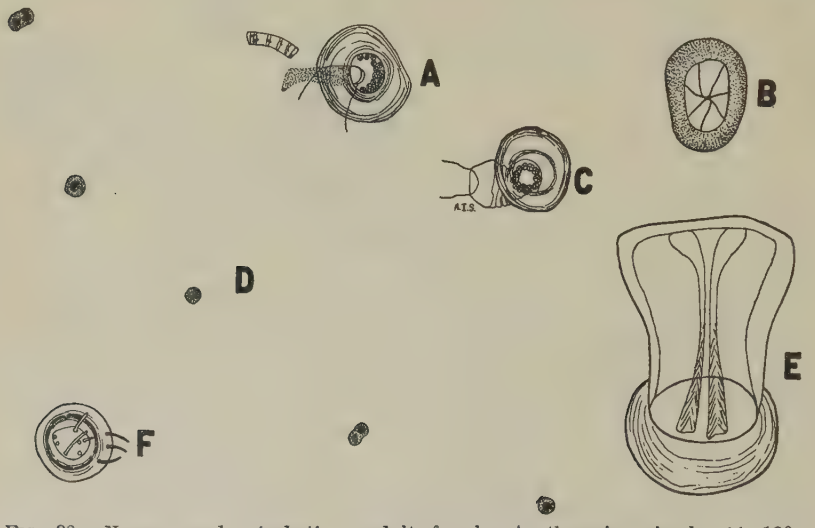

FIG. 29.—*Neomargarodes trabuti*, preadult female: A, thoracic spiracle, × 120; B, spiracular disk pore, × 1,500; C, abdominal spiracle, × 120; D, one set of ventral cicatrices, × 60; E, anal tube, × 330; F, antenna, × 120

much enlarged, trochanter, femur, and tibia-tarsus fused, claw large, stout, and elongate, posterior pairs of legs much more elongate, slender, the parts not fused, the claw very elongate, slender, nearly straight, claw digitules elongate tapering setae, very evident, but much shorter than the claw itself; beak fairly evident, placed between the anterior pair of legs, one-segmented, the framework of the mouth parts large, placed about opposite the middle pair of legs; thoracic spiracles of moderate size, each with a single large disk pore, normally with six loculi, within atrium; abdominal spiracles much smaller, but still quite conspicuous, apparently in seven distinct pairs, in contrast to the adult female, the posterior pair cylindrical tubes, each, except apical, with a smaller disk pore at inner end of first section; without derm pores; with a single pair of elongate apical setae, these, when perfect, exceeding the body in length, with a few small, slender setae dorsally, and with a few others, much longer but very slender, ventrally, these in segmental arrangement; anal opening subapical, simple, with a small, somewhat chitinized, elongate tube attached; apparently, but not certainly, with a single, relatively large, circular, ventral cicatrix, placed quite close to posterior apex.

Adult male (from literature only).—Elongate, but rather stout; apex of head triangular; antennal bases placed close together, antennae seven-segmented, three intermediate segments with long lateral branches, the antennae thus

conspicuously pectinate; compound eyes large, the facets large, the eyes elongated dorso-ventrally, contiguous below; anterior legs much enlarged as in Margarodes, the tibia, tarsus, and claw fused and resembling an enlarged claw, posterior pairs of legs slender, practically normal; wings broad, the outer section of the costal margin distinctly serrate, the basal diagonal arising very close to wing base, no trace of the apical diagonal found in some Margarodes; halteres distinctly broadened and flattened, with a single stout, acute, apical seta; abdomen probably with chitinized darker derm plates, apex tapering strongly, no suggestion of apical or lateral fleshy tassels, with two transverse clusters of tubular pores dorsally just before the apex of the abdomen; penis sheath stout and broad, other details of structure uncertain; abdominal

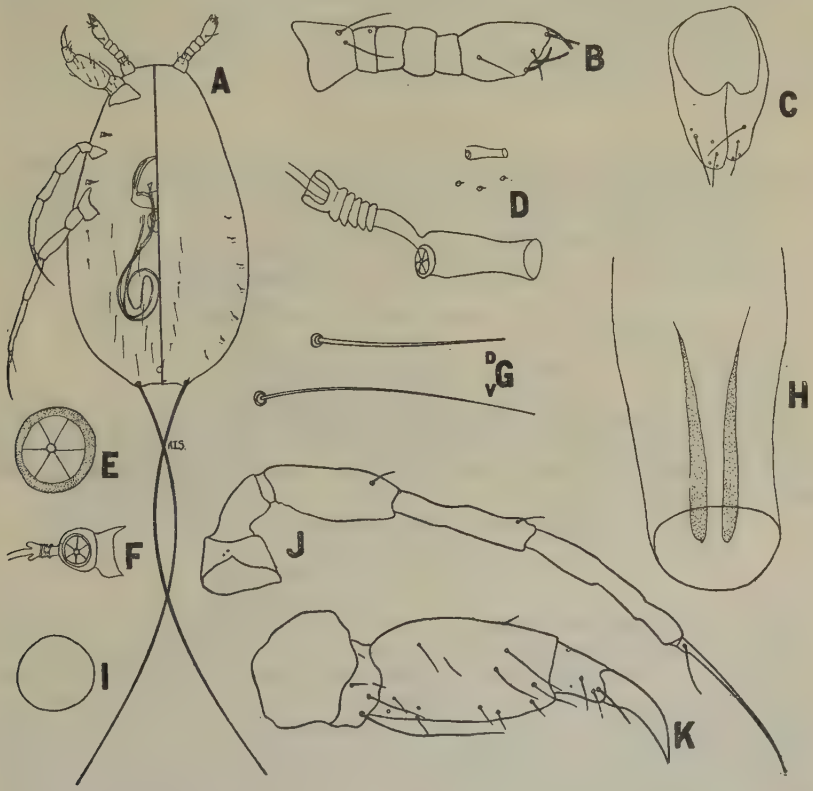

FIG. 30.—*Neomargarodes trabuti*, larva: A, outline, dorsal and ventral, × 60; B, antenna, × 230; C, beak, × 230; D, abdominal spiracle, above × 120, below × 1,500; E, thoracic spiracular disk pore, × 1,500; F, thoracic spiracle, × 460; G, derm setae, (D) dorsal and (V) ventral, × 650; H, anal tube, × 1,500; I, ventral cicatrix, × 330; J, middle leg, × 230; K, anterior leg, × 230

spiracles very evident, number uncertain, probably as in other stages, derm pores uncertain; with some fairly evident slender setae.

The known distribution of the genus, including as it does North Africa and India, covers the Mediterranean subregion of the Palaearctic region and the Indian subregion of the Oriental region.

Three species are assigned here, one, the genotype, *erythrocephala* Green (*70, p. 263*), known only from the adult male, the second, *trabuti* Marchal (*120, p. 1092*), known in all of the stages considered here, and the third, previously known as *Margarodes niger* Green

(*67*, *p. 75*), now transferred to this genus on the basis of a study of specimens determined by Green, its author, known in adult and preadult female stages.

KEYS TO SPECIES OF NEOMARGARODES

Adult female

a. Disk pores within opening of each abdominal spiracle few, small, inconspicuous, poorly developed, wanting in posterior pair and probably sometimes in others; heel of claw at most only very slightly swollen, its terminal portion narrowed and curved toward base of leg---*trabuti* Marchal

aa. Disk pores within opening of each abdominal spiracle, while never numerous, larger, distinctly developed, normally present in all spiracles; heel of claw plainly swollen and protruding, its outer apex bluntly rounded ----------*niger* (Green)

Preadult female

a. Ventral cicatrices arranged in a single median row of two or more and two lateral rows diverging from anal opening, each of these normally composed of, first, a single cicatrix, then three sets, each composed of two well separated ones, then another single one---------- *trabuti* Marchal

aa. No median row of ventral cicatrices, lateral rows made up of single cicatrices or, if of two, then these practically contiguous----- *niger* (Green)

No other stages of both species are available for examination.

TRIBE CALLIPAPPINI HANDLIRSCH

This tribe was established recently by Handlirsch (*90*, *p. 1036*) on the basis of the subfamily Callipappinae of MacGillivray (*119*, *p. 95*). Its usage in this paper coincides exactly with that of these authors.

GENUS CALLIPAPPUS GUÉRIN-MÉNEVILLE

(Pl. 2, D, and figs. 31, 32, and 33)

This genus was established by Guérin-Méneville (*81*, *p. 129*) many years ago for the reception of an unusual coccid from West Australia to which was given the specific name *westwoodi*. Species have been added from time to time, until there are now at least five, and perhaps six, presumably valid species included within the genus. The genus as a whole has recently been discussed by Froggatt (*56*, *p. 41*) and by the writer (*138*, *p. 41*) and a key to the adult females, the only stage known for some of the species, has been attempted by the latter. This key is repeated below following the generic discussion.

GENERIC CHARACTERISTICS

Habit.—Habit during the growth period not known; adult females clasping leaves or twigs on host (?) trees and becoming stationary at oviposition time.

Adult female.—Size large, body elongate-elliptical in shape; derm at maturity heavily chitinized, with large clear areolae surrounding individual pores and bases of setae, and with only the three anterior abdominal segments exposed, the remainder deeply invaginated to form a large internal marsupium with an opening placed at, from the external appearance, the posterior apex of the body, and not in the midventral abdominal region as in other coccids having marsupial pouches; antennae normally 10-segmented, the basal three enlarged, the second usually with around six sensory pores, the remaining segments gradually more elongate and more slender, apical longest of all; legs large and stout, suggesting those of Xylococcus, setae rather numerous, trochanter with numer-

ous (up to 16) small sensory pores on each face, tarsus quite plainly one-segmented, often more or less curved, claw large, stout, strongly curved, bearing several slender digitules in two clusters at base, these not knobbed at apices and much shorter than claw, no claw denticle; beak and mouth parts apparently sometimes very incompletely formed, situated between anterior legs; thoracic spiracles large, without bar, with large and conspicuous pore band bearing many small disk pores in atrium; abdominal spiracles in eight pairs, tubular, likewise large and conspicuous, except the last two pairs, these without pores and often much reduced in size, and inconspicuous, the remainder with double to triple band of small disk pores near inner end; derm bearing a single type of pore, this multilocular disk, with around six to eight loculi and circular center; no spines on derm; derm setae ordinary, slender, small, distributed over whole body but not crowded; derm hairs still smaller, but stouter, peculiarly invaginated for about half the length within a flask-shaped internal cup, these present over most of body, but relatively abundant only over that portion of the derm forming the marsupium, and particularly at the inner end of this, that is, the anatomically posterior end of the body; anal tube short, definitely developed, but not heavily chitinized, with simple ring at inner end; no evident ventral cicatrices.

Intermediate female.—Wholly unknown.

Larva.—Nearly uniformly elliptical; derm membranous; antennae 6-segmented, short and stout, placed close together on apex of head, but not con-

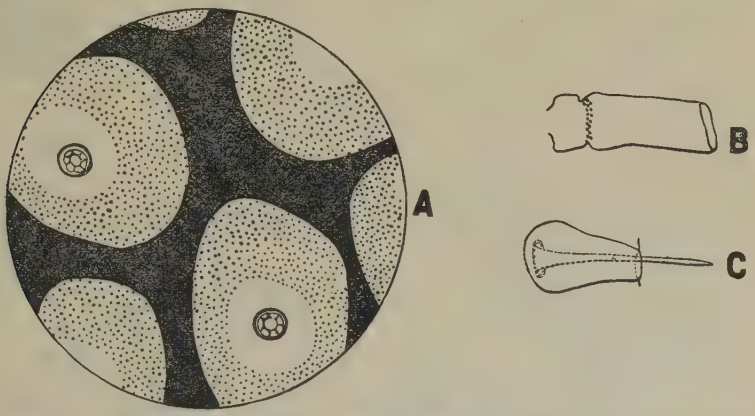

FIG. 31.—*Callipappus australis,* adult female: A, section of dorsal derm, × 220; B, abdominal spiracle, × 57.5; C, invaginated hair, × 530

tiguous, all segments except terminal broad and short, terminal ovoid, broadest at base, second segment with a single sensory pore, second and third segments each with one to several conspicuous, lanceolate, spinelike setae, all setae stout, none definitely differentiated as sensory setae; legs stout, trochanter with two sensory pores on each face, tarsus one-segmented, claw elongate, slightly curved, no denticles, without digitules of any sort; beak stout conical, possibly obscurely two-segmented, apical setae acute; thoracic spiracles of moderate size, each accompanied by a large internal pore plate bearing perhaps eight multilocular disk pores having around nine loculi each, and with a very faintly developed bar; abdominal spiracles very small and inconspicuous, located only with great difficulty, and only seven pairs noted; derm with minute, apparently bilocular pores along the body margin and with a circle of large multilocular disk pores around the apical anal opening, each of these with about 14 loculi; body bearing rows of small setae dorsally and ventrally and a series of relatively very large and conspicuous marginal setae on the abdominal segments, these setae having a length perhaps one-fourth that of the body; no spines, but with two small clusters of hairs ventrally at posterior apex of body near anal opening; anal opening apical, the internal tube fairly elongate, somewhat expanded medially, but without ring at inner end or pores at any point; no traces of ventral cicatrices.

Adult male.—Relatively large, as compared with males of other genera, and stout; apex of head triangular in outline; antennae elongate, first segment

large, somewhat gibbous within, second smaller, third approximately cylindrical, but much shorter than following segments, remaining segments elongate, slender, nearly cylindrical, irregularly nodulose, bearing slender, not very elongate setae; legs large, elongate, no bifurcate setae, trochanter with numerous (about 15) sensory pores on each face, tarsus long, somewhat curved, distinctly two-segmented, claw stout, slightly curved, claw digitules small, acute, set about one-third of claw length from base and less than one-third as long as claw; wings large, broad, slightly dusky, the costal complex narrowed to a point at its apex, but not continued to the wing tip, the two pale diagonal lines visible, the diagonal vein distinct, nearly straight, approaching closely to the wing margin; halteres very broadly expanded, almost leaflike, apparently with a single short, stout, apical seta; abdomen in mounted specimens somewhat broader about the middle, derm membranous in part, but with large, transverse, segmental, brownish, chitinized plates on the median line dorsally and ventrally; no suggestion of apical fleshy tassels; abdominal spiracles not certain; derm bearing marginal clusters and dorsal and ventral segmental rows of large, stout, sometimes almost spinelike setae, these accompanied by similar clusters and rows of small pores,

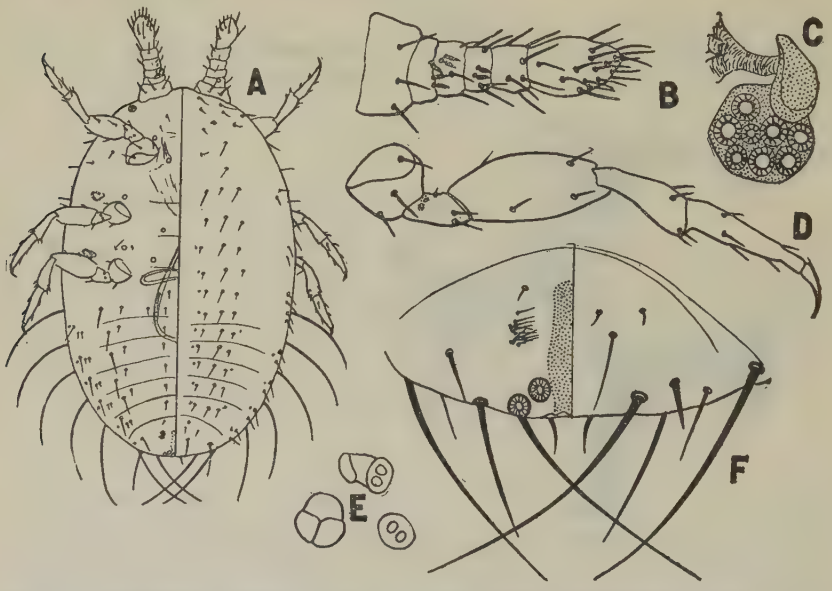

FIG. 32.—*Callipappus australis*, larva: A, outline, dorsal and ventral, × 57.5; B, antenna, × 165; C, thoracic spiracle, × 540; D, leg, × 165; E, derm pores, × 1,500; F, apex of abdomen, dorsal and ventral, × 230

mostly with bilocular or trilocular centers, and without, so far as can be determined, additional submarginal loculi; with two large transverse clusters of tubular ducts dorsally near apex of abdomen, these producing a large "brush" of glassy threads; penis sheath broad and stout at base, tapering abruptly to a deeply cleft, broadly bilobed apex, with ventral valve apparently lacking; fleshy penis very elongate, approximating the length of the body.

The genus is wholly Australian in its distribution, and occurs there, to judge from the scattered records, throughout the continent.

Nothing whatever seems to be known regarding the details of the life history of this insect. Specimens of the females have been found on a number of different plants, but no direct host relationship seems to have been proven in any of these records. The intermediate stages between larva and adult remain unknown.

The following species have been included here: *australis* (Maskell) (*123, p. 280*), originally described as Coelostoma, and reported from

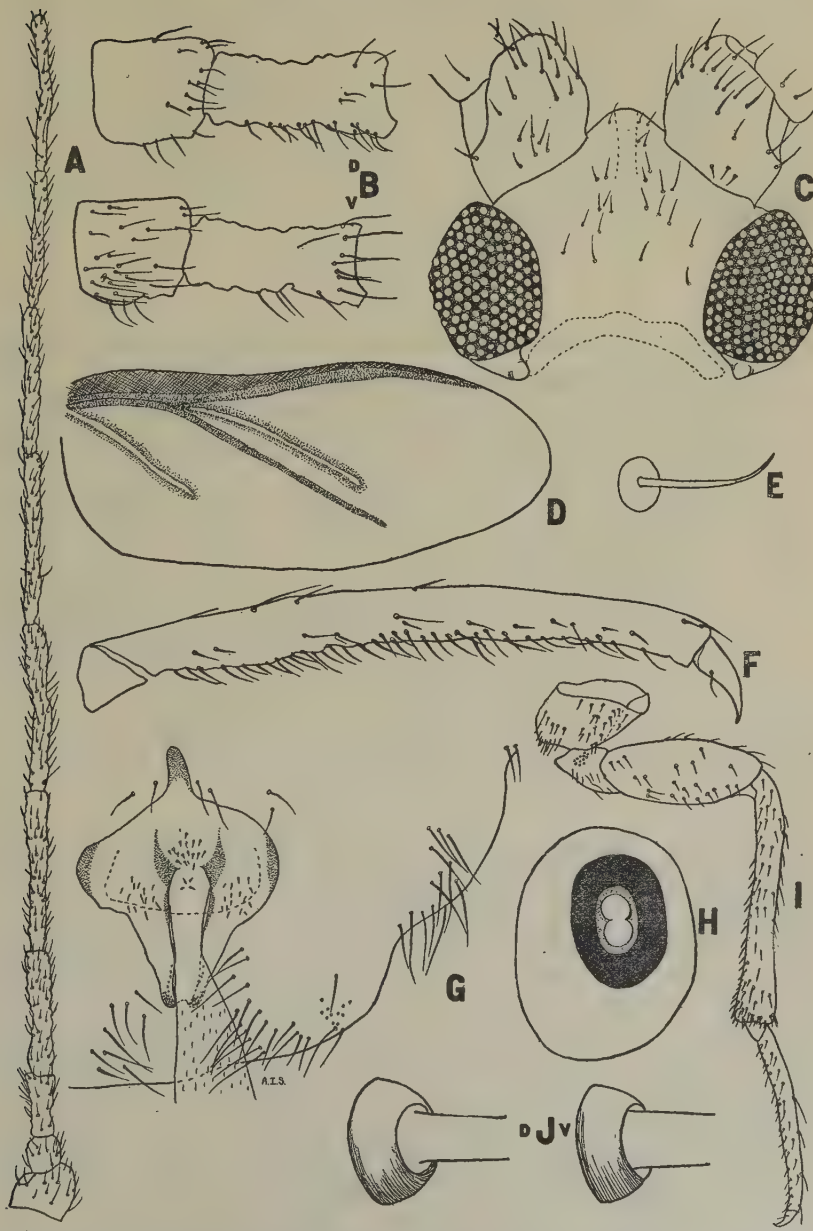

FIG. 33.—*Callippus australis*, adult male: A, antenna, × 17.5; B, same, second and third segments, dorsal (D) and ventral (V), × 60; C, head, dorsal, × 60; D, wing, × 7.5; E, dorsal body seta, × 650; F, tarsus and claw, × 60; G, apex of abdomen, × 50; H, dorsal abdominal derm pore, × 1,500; I, leg, × 12; J, dorsal (D) and ventral (V) submarginal bases of setae, × 650

New South Wales and Queensland; *farinosus* Fuller (*58, p. 1346*), reported on a species of Casuarina from West Australia, of which *C. bufo* Fuller (*58, p. 1346*) is a synonym according to Froggatt (*56, p. 42*); *immanis* (Maskell) (*124, p. 49*), described as Coelostoma, found on Acacia in central Australia; *rubiginosus* (Maskell) (*126, p. 242*), described as Coelostoma, and found on Banksia in Victoria and South Australia; and *westwoodi* Guérin-Méneville (*81, p. 129*), reported on Eucalyptus from West Australia.

A key to the adult females prepared and published by the writer (*138, p. 43*) is reproduced herewith.

KEY TO SPECIES OF CALLIPAPPUS

Adult female

a. External opening of abdominal pouch located ventrally near posterior apex of body (Fuller)----------*westwoodi* Guérin-Méneville
aa. External opening of abdominal pouch apical, not ventral.
b. Body more or less completely clothed (depending on condition) with brick to orange red, hairlike filaments----------*rubiginosus* (Maskell)
bb. Body without such filaments, bare or with whitish waxy or glassy secretion.
c. External opening of abdominal pouch a linear transverse slit.----------*farinosus* Fuller
cc. External opening of abdominal pouch circular to triangular or roughly 8-shaped.
d. Opening roughly 8-shaped; derm coarsely and uniformly punctured----------*australis* (Maskell)
dd. Opening circular to inverted triangular; derm finely punctured----------*immanis* (Maskell)

SUBFAMILY COELOSTOMIDIINAE MORRISON

The writer (*136, p. 102*) has very recently established this subfamily for the reception of the tribes and genera discussed below.

SUBFAMILY CHARACTERISTICS

Habit.—Usually forming a heavy globular test during the growing period, with the adult female retained within this and ovipositing inside of it; rarely naked but with the preadult very heavily chitinized at maturity, or protected only by secretion, or concealed beneath the host bark.

Adult female.—Body globular to stout elliptical, or ovoid to elongate elliptical; derm membranous or with heavily chitinized areas on head; antennae varying from flat plates bearing a few sensory setae to elongate, 10-segmented to 11-segmented, in the latter case the second segment with a single sensory pore, and usually with some sensory setae on the preapical as well as the apical segments; legs well developed or reduced to more or less elongate cones, well or poorly formed, trochanter with two to three sensory pores on each face, tarsus one-segmented, claw with or without denticle, claw digitules knobbed and exceeding claw apex, or acute and not attaining claw apex, apparently wanting in one genus; beak present or wanting, medium to elongate conical, more than one-segmented; thoracic spiracles with bar, without disk pores within atrium, but with disk pores at opening, slightly to distinctly larger than abdominal; abdominal spiracles so far as known in seven pairs, these the posterior ones, with or without pores within atrium; derm pores present, these multilocular disk, showing some variation in details of internal arrangement; derm with or without spines, without disks or disklike pores, with hairs and with setae, all of these mostly relatively abundant; anal opening apical, the tube well developed, large, with definitely formed ring at inner end, or small, narrow, without ring; no ventral cicatrices.

Intermediate female.—Body globular to elongate ovoid; derm membranous or more or less chitinized at posterior end; antennae either fully developed,

elongate, seven-segmented to nine-segmented, or reduced to stout conical form, but retaining marked evidence of segmentation; legs fully developed or reduced to more or less elongate conical tubercles or to flat plates, but retaining most of the joints even with reduction, except in the last case, claw with or without denticle, claw digitules present, acute, not attaining claw apex; beak present, well developed, moderately elongate to elongate conical, two-segmented, or, mostly, distinctly three-segmented; thoracic spiracles with bar, without disk pores within atrium, but with a pore cluster at opening of each, without tiny setae near opening of each; abdominal spiracles in the seven posterior pairs, except one genus, this with eight pairs, with the posterior pair poorly developed, with or, rarely, without pores within atrium; derm pores present, of the multilocular disk type, varying much in internal details; derm with spines, rarely without these, with hairs and setae, the vestiture mostly relatively dense; anal opening apical, the tube usually well developed and mostly with polygonal wax pores and multilocular disk pores near inner end, rarely without these, but with simple ring, or sometimes poorly developed and without ring; ventral cicatrices usually present in numbers, rarely wanting.

Larva.—Body elliptical to elongate elliptical; derm membranous or with the posterior apex chitinized; antennae stout, six-segmented, or, rarely, seven-segmented, the third segment usually very short, apical segment only bearing sensory setae; legs normal, claw usually with, rarely without, denticle, claw digitules knobbed and surpassing the claw apex, or acute and not attaining claw tip; beak attached opposite anterior legs, elongate conical, distinctly three-segmented, possibly rarely two-segmented (uncertain); thoracic spiracles with bar, mostly without, rarely with, disk pores within atrium, mostly with a disk pore or pores at opening; abdominal spiracles in seven pairs (one genus uncertain, perhaps with eight), these the posterior ones, rarely with pores within atrium, these usually wanting; derm with multilocular disk pores; with or without spines, with or without circular disks, with some hairs at least; apical setae only rarely (one genus) undifferentiated, usually with at least one and sometimes with more hairs present, anal opening apical, tube usually well developed and with a ring of pores at inner end, sometimes with neither pores nor chitinized ring at inner end.

Adult male (based on New Zealand forms only).[16]—Of the usual elongate shape; head acute between antennal bases, antennae simple, moderately stout, apical segment shortest; midthoracic dorsal area with a conspicuous, transverse, elliptical or oblong, clear unchitinized area; legs with bifurcate setae on tibia, trochanter with three to four sensory pores on each face, tarsus distinctly two-segmented, claw with denticle, claw digitules knobbed and attaining or surpassing the claw apex, or slender, acute, not attaining it; wings relatively narrow, the basal diagonal short, costal complex truncate well before wing apex, apical diagonal wanting; halteres narrow, sometimes expanded at apices, each with three or four elongate, hooked, knobbed, apical setae; abdomen without heavy, transverse, chitinized plates, without subapical dorsal clusters of large tubular pores; with distinctly developed disk pores; penis sheath stout at base, tapering to a moderately elongate to very elongate tip, this entire or cleft and bilobed, the ventral valve short and straight.

The distribution of the subfamily as here constituted is somewhat anomalous, in that a single genus included comes from the Mediterranean subregion of the Palaearctic region, while all the remainder come from the Neotropical region or from the New Zealand subregion of the Australasian region. Information regarding the European genus is not complete and some change in the status given to it here will doubtless prove necessary at some future date.

There is no precise information published, and probably none known, regarding the life history of any of the included species.

Three tribes have been placed in this subfamily. The available information regarding two of these is incomplete and inadequate, and a study of additional stages, in particular of the adult male, when available, will doubtless demonstrate that some changes in

[16] See footnote 17.

assignment will be required. The different stages of these, so far as known, may be separated by the following keys:

KEYS TO TRIBES OF COELOSTOMIDIINAE

Adult Female

a. Anal tube small, definitely chitinized but without traces of ring or pores at inner end; legs and antennae fully developed, claw digitules acute and not attaining claw tip ..... Marchalinini

aa. Anal tube of fair size to large, membranous, but with a distinct or fairly distinct ring at inner end (assumed in case of Platycoelostomini, information on which is very incomplete); legs, if well developed and of normal length, with the claw digitules knobbed and mostly surpassing claw apex.

b. Derm without hairs (based on small portion of derm of cephalic region only) ..... Platycoelostomini

bb. Derm with hairs ..... Coelostomidiini

Intermediate Female

a. Legs reduced to flat, elongate ovoid plates on surface of ventral derm near thoracic spiracles, without definitely formed claw or digitules; with eight pairs of abdominal spiracles, the posterior pair incompletely developed; derm pores of a distinct type, large, flat, with very large simple center and submarginal band of numerous loculi ..... Platycoelostomini

aa. Legs at least developed as distinct stout cones with definite claw at apex of each; with seven pairs of abdominal spiracles, these the posterior pairs; derm disk pores smaller, with small circular to quadrilocular center.

b. Abdominal spiracles without pores within atrium; ventral cicatrices wanting; anal tube without ring and pores at inner end ..... Marchalinini

bb. Abdominal spiracles with pores within atrium; ventral cicatrices present, numerous, anal tube with ring and pores at inner end. Coelostomidiini

Larva

a. Antennae normally seven-segmented, at least one preapical segment with sensory setae; beak attached approximately opposite middle coxae; derm pores of two sorts, one large, similar to those of intermediate stage; with a single, rather large, median, ventral cicatrix ..... Platycoelostomini

aa. Antennae normally six-segmented, apical segment only with enlarged sensory setae; beak attached approximately opposite the anterior coxae; derm pores not resembling those of preceding tribe; without a ventral cicatrix or with three or more.

b. Abdomen without distinctly differentiated apical or lateral marginal setae, although with numerous setae; ventral cicatrices wanting. Marchalinini

bb. Abdomen with at least a single pair of distinctly differentiated apical setae, sometimes with more; ventral cicatrices present, three or more in number ..... Coelostomidiini

The adult male stage in this subfamily is known only in certain genera of the tribe Coelostomidiini.

TRIBE PLATYCOELOSTOMINI MORRISON

This tribe has been erected (*136, p. 102*) for the single New Zealand genus Platycoelostoma Morrison.

Tribal Characteristics

The characters given below for this genus will also serve to define the tribe. In the absence of complete adult female specimens and

of adult males, the true relationships of the genus and tribe remain obscure, and their present assignment must be regarded as tentative.

Genus Platycoelostoma Morrison

(Pl. 2, E, and figs. 34, 35, and 36)

This genus was established by the writer (*138, p. 34*) to receive a species, *compressa*, described from New Zealand by Maskell as a Coelostoma. Although certain morphological features are of much interest, it is impossible to place the genus with any precision in the absence of whole specimens of the adult female and specimens of the adult male stages.

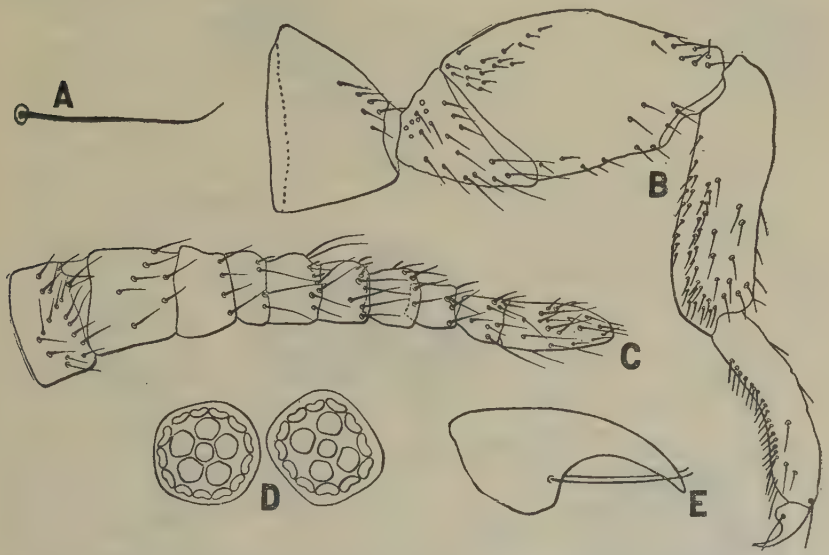

Fig. 34.—*Platycoelostoma compressa*, adult female: A, body seta, × 500; B, leg, × 57.5; C, antenna, × 57.5; D, derm pores, × 1,500; E, claw, × 220

GENERIC CHARACTERISTICS

Habit.—Living during the growing period concealed in pockets formed beneath the outer bark of the host. Oviposition habit in nature not known.

Adult female (based on antennae, anterior legs, and small portion of derm only).—Body elongate elliptical; antennae placed rather close together at apex of head, 10-segmented, tapering somewhat, second segment, so far as can be determined, with only a single sensory pore, apical segment longest and most slender, with perhaps two stout sensory setae at tip; legs ample, stout, each face of trochanter with four to six sensory pores, setae on legs fairly numerous, those on tarsus tending to be long and slender, claw stout and broad at base, with a slight heel, apical portion strongly curved, with two elongate, bluntly tipped denticles surpassing the apex of claw; beak wanting (Maskell); spiracles uncertain, presumably, from intermediate stage, with two pairs of thoracic and seven or eight pairs of abdominal; derm pores of one type, multilocular disk, with small circular center, four to five large loculi, and an outer circle of many small loculi (12 to 14); derm bearing slender setae, these fairly abundant; anal tube and ventral cicatrices uncertain.

Intermediate female (preadult).—Uniformly elliptical in outline; derm membranous, or somewhat chitinized at maturity; antennae greatly reduced, represented by small, slightly tapering tubercles, broadly rounded at tips, bearing numerous stouter setae at apex and showing very faint indications of segmenta-

tion; legs present only as flat, somewhat differentiated areas in the derm, bearing some short and some longer stout setae; beak small, conical, two-segmented; thoracic spiracles of moderate size, with narrow bar and large opening, with a large band of disk pores within atrium; abdominal spiracles in seven pairs, these well developed, large tubular, each with a double band of disk pores near inner end, and an eighth pair smaller, simple, without disk pore band; derm pores of a single sort, very large, circular, with unmodified or granular center and a submarginal band of numerous loculi (up to 30) with a slight thickening and an inner pore at one point, these pores rather abundant on both surfaces, more numerous along body margin; derm setae present, in general short and tending to stoutness, some distinctly lanceolate, not so numerous as pores, but

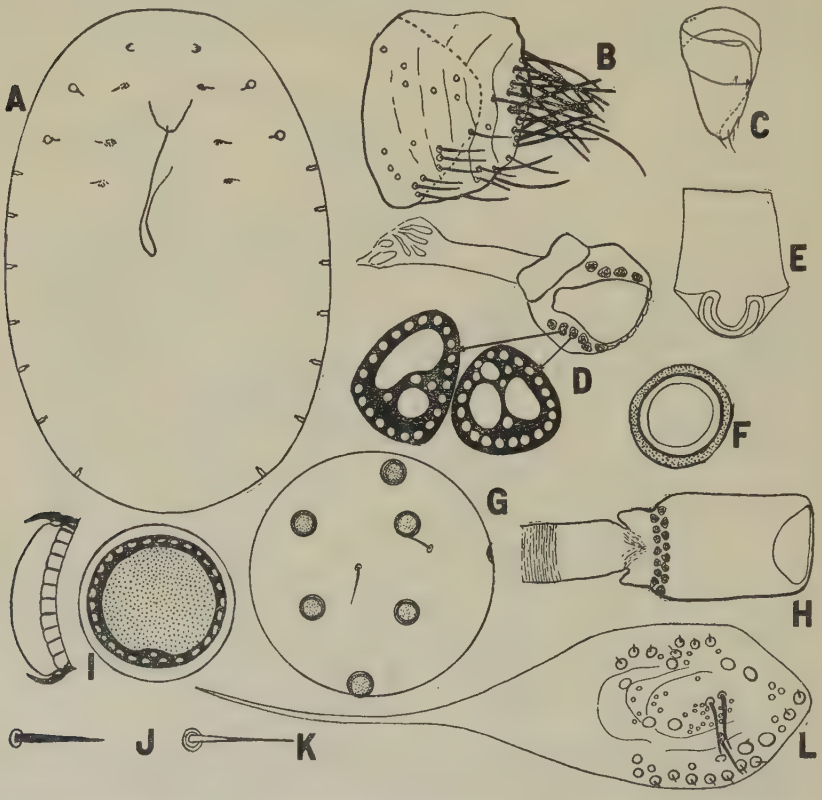

FIG. 35.—*Platycoelostoma compressa*, preadult female: A, outline, × 17.5; B, antenna, × 500; C, beak, × 60; D, thoracic spiracle, × 220, with detail of pores, × 1,500; E, anal tube, × 165; F, ventral cicatrix, × 1,500; G, section of ventral abdominal derm, × 220; H, abdominal spiracle, × 220; I, derm disk pore, surface and side, × 1,500; J, derm seta, × 500; K, derm seta, × 650; L, middle leg, × 1,500

widely distributed; anal opening nearly apical, tube membranous, with a fairly heavy ring at inner end, this apparently without pores; ventral cicatrices present, small, circular, in small clusters on each half of the abdomen only, so far as can be determined.

Larva.—Body very elongate elliptical; antennae placed close together at anterior apex of head but not contiguous, fairly stout, distinctly seven-segmented, the intermediate short, terminal longest, apical and preapical bearing a stout sensory seta; legs stout, the anterior slightly stouter than the others, the parts with few setae, trochanter with two pores on each face, claw rather slender, somewhat curved, with a distinct denticle near apex, with two long, conspicuously knobbed digitules, these exceeding the tip of the claw; beak placed nearly opposite middle legs, elongate conical, distinctly two-segmented,

the apical sensory setae acute; thoracic spiracles large, opening transverse, with several quadrilocular to quinquelocular disk pores within opening of each, and with bar; abdominal spiracles uncertain; derm pores of two distinct types, both large, one with large simple center and submarginal band of small loculi, the other with 7 to 11 large loculi and simple or bilocular or trilocular centers; derm bearing a fair number of setae of small to moderate size, and with a single pair of larger apical setae, these, however, hardly one-tenth the length of the body; anal opening apical, the tube simple, somewhat chitinized, thickened at inner end, but, so far as can be determined, without pores at any point; with a single large, circular, median, ventral cicatrix.

Only the type species, a New Zealand form found in the immature stages beneath the bark of Podocarpus, has been included in the genus.

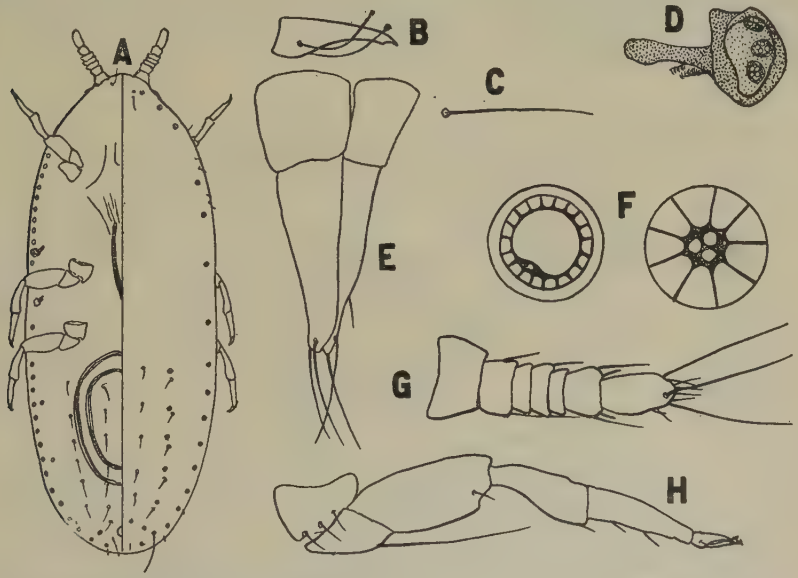

FIG. 36.—*Platycoelostoma compressa*, larva: A, outline, dorsal and ventral, × 57.5; B, claw, × 640; C, derm seta, × 500; D, thoracic spiracle, × 1,500; E, beak, × 230; F, derm pores, × 1,500; G, antenna, × 57.5; H, leg, × 57.5

Nothing precise is known regarding the life cycle of the insect. Maskell (*124, p. 46*) claims that it is able to reproduce parthenogenetically, as he obtained, from the immature females kept in confinement on bark, first adult females, then, later on, larvae from these females. No male stages were involved in any way, according to him.

TRIBE MARCHALININI MORRISON

As recently characterized by the writer (*136, p. 102*), this tribe includes only one genus, Marchalina Vayssière.

TRIBAL CHARACTERISTICS

The generic definition given below will serve to indicate the characteristics of the tribe as well as of the genus.

Genus Marchalina Vayssière

(Pl. 2, F, and figs. 37, 38, and 39)

This genus was only recently characterized by Vayssière (*168, p. 427*), who assigned as its type and only included species the insect originally described as *Monophlebus hellenicus* Gennadius (*59, p. 32*) but more recently associated with the genus Palaeococcus. When erected, the genus was placed in the subfamily Monophlebinae, but, in the opinion of the writer, it is more satisfactorily placed in the group to which it is here assigned. It is another of those intermediate or connecting forms that bridge any gaps that appear between the extremes in the subfamilies here considered and, from our present knowledge, is possibly the closest to the Monophlebinae of any of the genera excluded from that subfamily.

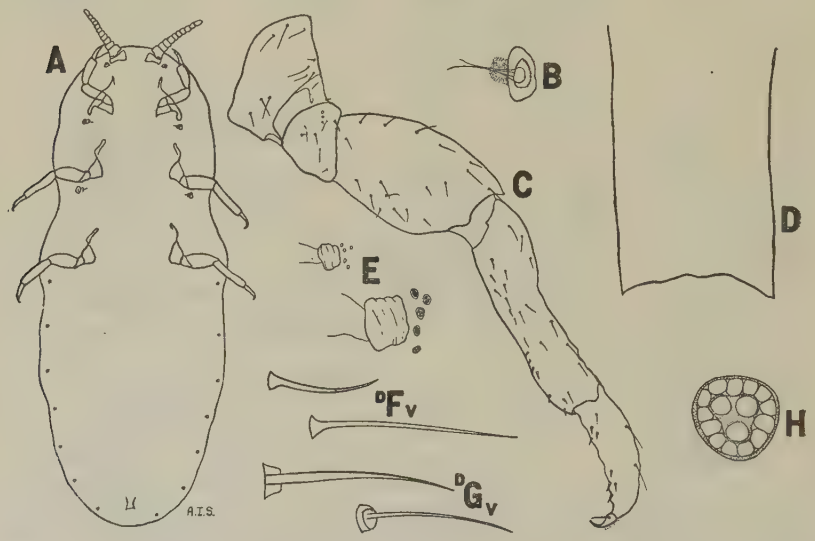

Fig. 37.—*Marchalina hellenica,* adult female: A, outline, optical section, × 7.5; B, thoracic spiracle, × 60; C, leg, × 50; D, anal tube, × 165; E, abdominal spiracle, above × 60, below × 120; F, derm hairs, (D) dorsal and (V) ventral, × 650; G, derm setae, (D) dorsal and (V) ventral, × 650; H, derm multilocular disk pore, × 1,500

GENERIC CHARACTERISTICS

Habit.—Exposed on host during period of growth; at oviposition producing a dense mass of felted secretion beneath the body for the protection of the eggs.

Adult female.—Body elongate elliptical; derm membranous throughout; antennae 11-segmented (Vayssière), second with a single sensory pore, the segments from the fourth on bearing one or more large, stout, sensory setae; legs stout, trochanter with only two or three sensory pores on each face, no spinelike setae, claw slender, elongate, somewhat curved, finely denticulate within toward apex, claw digitules developed, slender at tips, not attaining apex of claw; beak wanting, or perhaps very imperfectly developed, represented by folds in some cases, mouth parts wanting or very incompletely developed in some cases; thoracic spiracles only moderate in size, with weakly formed bar and row of disk pores outside the opening, but none within; abdominal spiracles in seven pairs, these the posterior ones, all short tubular, much smaller than thoracic, but quite evident, without pores within atrium, but with some disk pores at mouth; derm pores of a single type, multilocular disk, with central circular to oval area having two or three widely separated circular loculi and a marginal band of perhaps 16 to 17 small loculi; derm bearing some setae of moderate size, these

widely distributed; with numerous hairs, these likewise of moderate size; derm without spines in this stage; anal opening apical, the anal tube of moderate length, somewhat chitinized, without pores or thickened ring at inner end or elsewhere; no ventral cicatrices.

Intermediate female (preadult).—In general resembling the adult female in most respects; body elongate elliptical or elongate ovoid, broader behind; derm membranous; antennae usually nine-segmented, segments beyond fourth with one or more stout sensory setae, second segment with a single sensory pore; legs stout, fully developed, bearing slender setae, trochanter with three sensory pores on each face, claw stout, somewhat curved, faintly denticulate within near tip, digitules slender, acute at tips, not quite attaining claw apex; beak elongate conical, distinctly three-segmented, basal segment distinct, tip with several acute apical setae; thoracic spiracles large, with distinct bar and a few pores clustered at opening of each; abdominal spiracles in seven pairs, the anterior lacking, each strongly expanded within opening but without disk pores, either within or externally and intimately associated with the opening itself; derm pores of a single type only, these normally circular, with small circular center surrounded by about eight fairly large loculi; body bearing slender

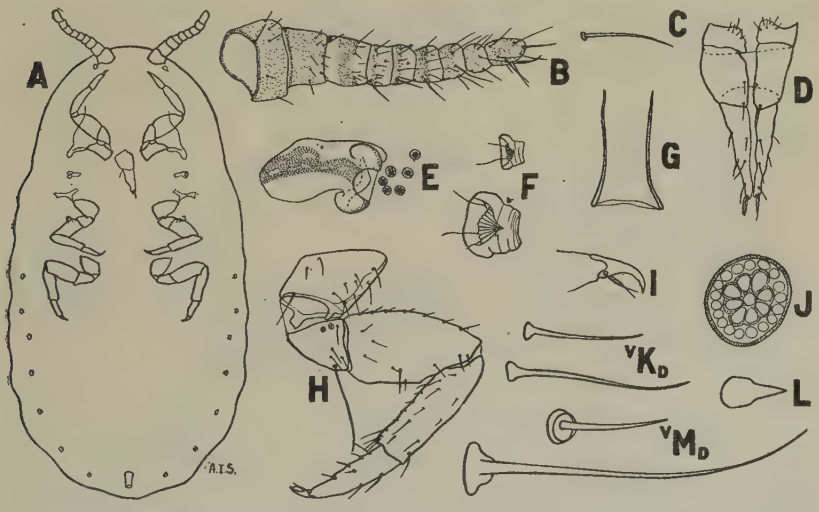

FIG. 38.—*Marchalina hellenica*, preadult female: A, outline, optical section, × 12; B, antenna, × 60; C, beak seta, × 230; D, beak, × 60; E, thoracic spiracle, × 120; F, abdominal spiracle, above × 120, below × 230; G, anal tube, × 165; H, leg, × 60; I, claw, × 120; J, derm multilocular disk pore, × 1,500; K, derm hairs, (D) dorsal and (V) ventral, × 650; L, derm spine, × 650; M, derm seta, (D) dorsal and (V) ventral, × 650

conical spines with enlarged bases along the margin and dorsally; in the posterior abdominal region bearing some setae of moderate size, these slightly longer along the body margin, and finally bearing numerous hairs, these distinctly smaller than the setae and nearly uniformly distributed over the body; anal tube apical, simple, without ring or pores at inner end, hence as in adult; ventral cicatrices wanting. Earlier stages closely resembling the preceding, but less developed.

Larva.—Body, as mounted, elongate elliptical; derm membranous; antennae placed fairly close together at anterior apex of body, not nearly contiguous at base, six-segmented, the second elongate, with a single large sensory pore at apex, next three very short, much wider than long, the terminal somewhat enlarged, elliptical with base truncate, terminal only with a single stout sensory seta; legs stout, bearing few setae, trochanter with two sensory pores on each face, claw slender, definitely curved, apparently without subapical denticle, with slender digitules, slightly knobbed at tip and slightly exceeding claw apex; beak elongate conical, distinctly three-segmented, the few apical setae acute; thoracic spiracles large, with bar, with a single disk pore at the mouth of each; abdominal spiracles in seven pairs, the anterior lacking, each of fair size, but

much smaller than the thoracic, each with enlarged atrium but without disk pores definitely associated; derm pores of a single type, circular multilocular disk, with small round center, and about five large loculi surrounded by a marginal circle of about 12 to 14 small loculi; derm bearing short spines, these slender conical with slightly rounded tips and enlarged bases; with some setae, these of moderate size but quite evident, none sharply differentiated as either an apical pair or as marginal pairs of setae; derm also with hairs, these slender, smaller than the setae, with strongly expanded bases; anal tube directly apical, opening not surrounded by a definite collar of disk pores, although with disk pores and spines frequent in the area around the opening, tube somewhat, but not heavily, chitinized throughout its length, simple, without pores or thickened ring at inner end; no traces of ventral cicatrices.

Adult male.—Not known.

The single included species is recorded from species of Pinus from the European territory bordering on the Ægean Sea, hence the genus comes within the Mediterranean subregion of the Palaearctic region.

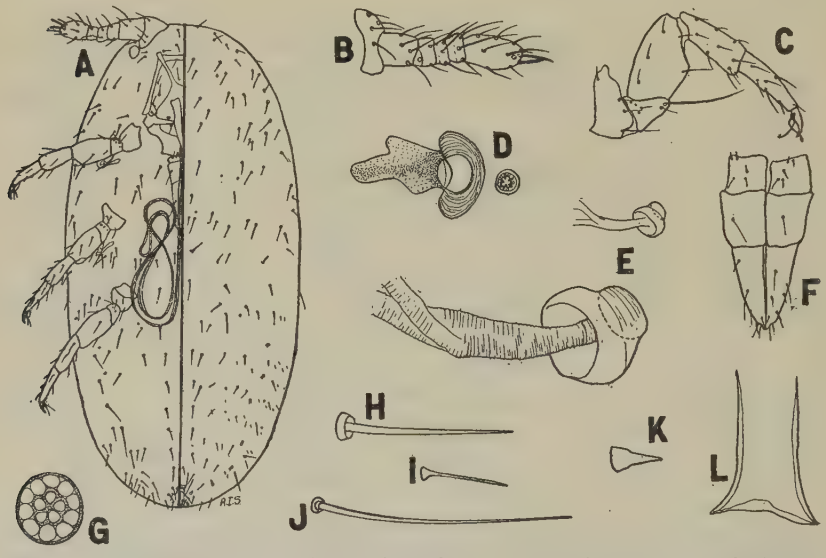

FIG. 39.—*Marchalina hellenica*, larva: A, outline, dorsal and ventral, × 60; B, antenna, × 115; C, leg, × 115; D, thoracic spiracle, × 460; E, abdominal spiracle, above × 460, below × 1,500; F, beak, × 115; G, derm disk pore, × 1,500; H, dorsal seta, × 650; I, ventral hair, × 650; J, ventral seta, × 650; K, dorsal spine, × 650; L, anal tube, × 330

Nothing seems to have been published regarding the life cycle of the genotype.

TRIBE COELOSTOMIDIINI MORRISON

The writer (*136, p. 102*) established this tribe recently for the reception of the five definitely related genera discussed below.

TRIBAL CHARACTERISTICS

Habit.—Enveloped during the growing period by a heavy-walled, nearly globular, presumably secreted test, or naked but with heavily chitinized preadult; adult female usually, but not always, retained within and ovipositing in the test.

Adult female.—Body globular to stout elliptical to somewhat elongate elliptical; derm membranous or with anterior apex heavily or posterior apex slightly chitinized; antennae well developed, of normal length, or reduced to short cones or even to flat plates, when well developed with sensory setae on preapical

as well as apical segments, second segment with a single sensory pore; legs well developed or more or less reduced to short cones, but in any case with claw and digitules distinctly developed, trochanter with only two to three pores on each face, tarsus one-segmented, claw with or without denticle, claw digitules knobbed and surpassing claw apex, or acute and not attaining claw apex, rarely wanting; beak rarely present, small, not well developed, if present rather elongate conical, two-segmented to three-segmented; thoracic spiracles with bar, without pores within atrium, but with disk pores on derm at opening; abdominal spiracles in the seven posterior pairs, these as large as thoracic to definitely smaller; derm disk pores present, multilocular, showing some variation in details of internal composition, derm with or without spines, without disks or disklike simple pores, with hairs, and with setae, vestiture relatively dense; anal opening apical, the tube well developed but not heavily chitinized, with a more or less definitely developed ring at inner end; ventral cicatrices wanting.

Intermediate female.—Body mostly globular or nearly so, derm membranous or more or less chitinized, particularly at posterior apex; antennae rarely fully developed and elongate, usually short conical with rounded apex, but in any event retaining definite evidence of segmentation; legs only rarely well developed and approximately normal in appearance, usually reduced to short to elongate cones, but retaining at least some evidences of division into parts, and with claw and digitules developed, the first with or without distinct denticle, the claw digitules not attaining the claw apex; beak elongate conical, usually distinctly three-segmented, rarely shorter and possibly only two-segmented; thoracic spiracles with bar, with disk pores on derm at opening, without tiny pores or setae on derm near opening; abdominal spiracles with the seven posterior pairs developed, each with disk pores within atrium; derm bearing multilocular disk pores, these of one general type, but showing some variation in internal organization; derm with or without spines, with hairs, and with setae, the vestiture relatively dense; anal opening apical, the tube well to very well developed, with pores and ring at inner end; ventral cicatrices present, small, circular, numerous, mostly in transverse segmental bands or rows.

Larva.—Body elliptical to elongate elliptical, derm membranous or with posterior apex chitinized; antennae well developed, stout, six-segmented, with enlarged sensory setae on apical segment only; legs normally developed, claw with denticle, claw digitules knobbed and exceeding claw tip or acute and not attaining claw tip; beak attached opposite anterior coxa, elongate conical, distinctly three-segmented; thoracic spiracles with bar, with one or more disk pores at opening, but none within atrium; abdominal spiracles present in the seven posterior pairs, with or without a disk pore within atrium of each; derm bearing multilocular disk pores, these showing some variation in internal organization; derm with or without spines, with or without flat disks or disklike simple pores, with hairs, vestiture relatively fairly abundant; with one or four pairs of elongate, differentiated, apical abdominal setae; anal opening apical, tube well developed, with ring, and one or more rows or bands of pores near inner end; with three or more ventral cicatrices.

Adult male (based on New Zealand genera only).[17]—The discussion of the subfamily characteristics of the adult male stage, as given above under that heading, coincides exactly with any characterization that might be given for the adult males of the tribe Coelostomidiini, and so may be referred to in this connection.

The distribution of the tribe, as here established, is definitely restricted to the New Zealand subregion of the Australasian region and to the Neotropical region.

The life cycle of no one of the included species has been worked out with any precise detail.

Five genera, one of which is newly described, have been assigned to this tribe. These fall very obviously into three groups, one including the two New Zealand genera, the second the two Neotropical genera known from Brazil and Mexico, and the third the newly described genus from the upper portion of the Chilean subregion of the Neotropical region.

[17] See footnote 18.

These genera may be separated by the following keys:

KEYS TO GENERA OF THE TRIBE COELOSTOMIDIINI

ADULT FEMALE

a. Derm wholly membranous; antennae and legs fully developed, normally elongate, the first 11-segmented; setae on tibia and tarsus quite stout, almost spinelike; derm not bearing spines ..... Coelostomidia

aa. With a heavily chitinized plate on the head, this rarely only faintly chitinized, or derm membranous with very slight to slight chitinization around anal opening; antennae and legs reduced to more or less elongate cones, or otherwise modified, but leg segmentation retained; antennae sometimes reduced to flat plates; setae on tibia and tarsus slender and few in number.

b. Antennae short conical, apices broadly rounded, five-segmented to seven-segmented; openings of thoracic and abdominal spiracles of approximately equal size.

c. Anterior apex of head, between and above antennal bases, with a faintly chitinized plate, remainder of derm membranous; claw digitules knobbed and surpassing apex of claw; derm not bearing spines ..... Ultracoelostoma

cc. Anterior apex of head and all of derm except posterior apex membranous, this last chitinized; claw digitules acute and not attaining apex of claw; derm bearing spines ..... Paracoelostoma

bb. Antennae reduced to mere plates, indistinctly differentiated from the heavily chitinized area inclosing them; openings of abdominal spiracles definitely smaller than those of thoracic pairs.

d. Legs elongate, but poorly formed, rather baglike, claw without denticle, claw digitules wanting ..... Mimosicerya

dd. Legs conical, not elongate, claw elongate, with several denticles, claw digitules present ..... Cryptokermes

INTERMEDIATE FEMALE

a. Antennae and legs fully developed, the first eight-segmented to nine-segmented; body globular, naked, heavily chitinized at maturity, with small round hole at posterior end; in appearance suggesting, and previously mistaken for, an adult form ..... Mimosicerya

aa. Antennae and legs, while showing segmentation, reduced to stout conical protuberances; body inclosed within a heavy-walled secreted test, not naked, not heavily chitinized.

b. Anal tube short, with polygonal wax pores at inner end, but lacking circle or band of disk pores near these ..... Paracoelostoma

bb. Anal tube elongate, with a circle or band of disk pores near inner end in addition to band of polygonal wax pores.

c. Legs reduced to flat conical stubs, the segmentation decidedly incomplete ..... Ultracoelostoma

cc. Legs elongate conical to about half normal size, the segmentation nearly complete.

d. Derm with multilocular disk pores, and with some with large trilobate center and not more than three small loculi. Coelostomidia

dd. Derm with disk pores with numerous loculi only, none as described above ..... Cryptokermes

LARVA

a. Posterior apex of abdomen strongly chitinized.

b. Ventral cicatrices in six pairs arranged in two longitudinal rows, one on each half of the ventral face of the abdomen ..... Paracoelostoma

bb. Ventral cicatrices three in number, arranged in a transverse row near posterior apex of body ..... Ultracoelostoma

aa. Posterior apex of abdomen not chitinized.
c. With a single pair of apical setae ..... Coelostomidia
cc. With four pairs of apical and subapical setae.
d. Spines near posterior apex of abdomen stout conical, tapering strongly to tips ..... Cryptokermes
dd. Spines near posterior apex of abdomen elongate, slender, intermediate portion nearly cylindrical, apices only tapering to point ..... Mimosicerya

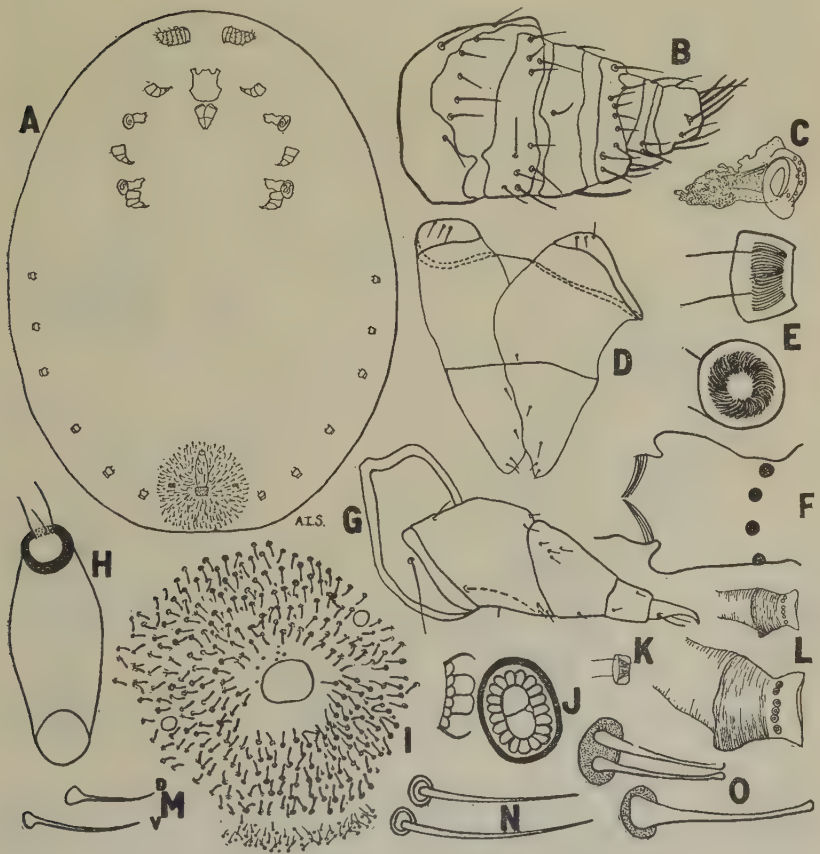

FIG. 40.—*Paracoelostoma peruviana*, adult female: A, outline, × 12; B, antenna, × 165; C, thoracic spiracle, × 60; D, beak, × 120'; E, posterior abdominal spiracle, two views, × 230; F, an anterior abdominal spiracle, × 230; G, leg, × 165; H, anal tube, × 60; I, cluster of setae around anal opening, × 60; J, derm disk pore, × 1,280; K, apical abdominal spiracle, × 60; L, intermediate abdominal spiracle, above × 60, below × 120; M, derm hairs, dorsal (D) and ventral (V), × 650; N, derm setae, ventral, × 650; O, derm spines, × 650

GENUS PARACOELOSTOMA MORRISON

(Pl. 3, A, and figs. 40, 41, and 42)

This genus has been established recently by the writer (*136, p. 102*) to accommodate a single South American species.

GENERIC CHARACTERISTICS

Habit.—Inclosed during the growing period within a heavy walled, globular test; adult female retained within this test and ovipositing therein.

Adult female.—Probably approaching globular in form; derm membranous, with the posterior apex, surrounding the anal opening, becoming slightly chitinized at maturity, the anal tube of the preadult often retained, no chitinized area on anterior apex of head; antennae much reduced, stout conical, more or less distinctly five-segmented or six-segmented, the apical and preapical segments bearing one or more enlarged sensory setae; legs similarly reduced, acutely conical, the joints separating the parts more or less distinct, with definite well-developed apical claw, somewhat curved, roughened on inner face, the digitules apparently acute, not attaining the tip of the claw; beak present, but not heavily chitinized, on this account indistinctly three-segmented, the basal segment quite narrow; thoracic spiracles fairly large, with wide bar and a small cluster of disk pores at mouth; abdominal spiracles quite large, somewhat smaller than thoracic, with a circle of disk pores within atrium of each, the apical pair smaller, set close to the anal opening; derm pores of a single multilocular disk type, slightly elliptical, with more or less distinctly bilocular center and numerous (around 16) small loculi, these well distributed over body, but more abundant, rather crowded, toward posterior end, spiracular

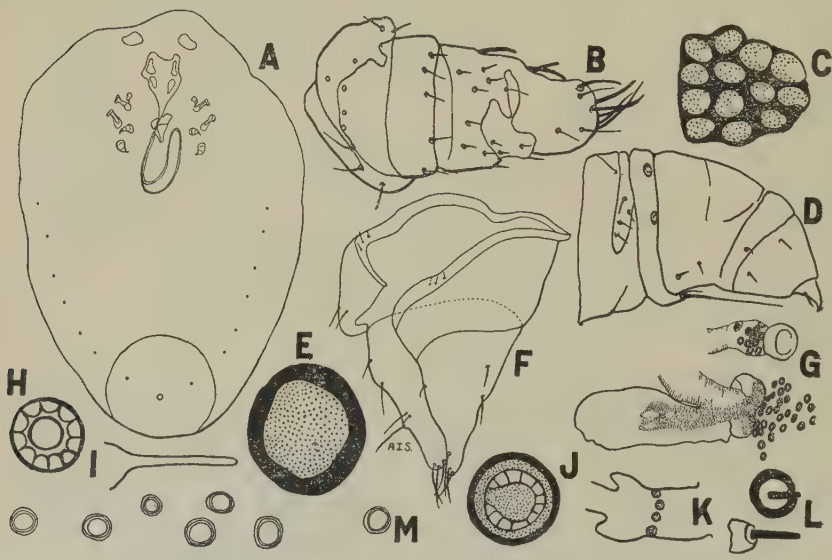

FIG. 41.—*Paracoelostoma peruviana*, preadult female: A, outline, optical section, × 12; B, antenna, × 230; C, section of derm showing areolations, × 530; D, leg, × 230; E, single ventral cicatrix, × 460; F, beak, × 120; G, abdominal (above) and thoracic (below) spiracles, × 120; H, derm disk pore, × 1,500; I, derm hair, × 1,500; J, derm disk pore, × 1,280; K, abdominal spiracle, somewhat diagrammatic, × 230; L, derm seta, × 1,500; M, portion of transverse row of ventral cicatrices, × 120

disk pores with fewer loculi; posterior apex of body with a circular cluster of elongate, rather slender, almost setalike spines, each with bluntly rounded, slightly clavate tip, surrounding the anal opening; with small, rather stiff setae scattered over body and with small, rather stiff hairs, each with expanded base, likewise scattered over body; anal opening apical; anal tube large, hardly chitinized, but with chitinized ring at inner end, often retaining the preadult anal tube; no ventral cicatrices.

Intermediate female (preadult).—Elliptical, probably approaching a globular form at maturity; apex of abdomen, around anal opening, heavily chitinized, remainder of derm membranous; antennae more or less definitely seven-segmented to eight-segmented, the segments narrow, the entire antenna stout at base, short conical, apex rounded or somewhat constricted; legs similarly reduced, acutely conical, parts more or less distinctly separated, claw well developed, somewhat curved, inner face roughened, claw digitules slender, apparently acute at tips, not nearly attaining claw apex; beak rather elongate conical, distinctly three-segmented, the basal narrow, with a few acute sensory setae at the apex; thoracic spiracles fairly large, with bar and cluster of

pores at mouth; abdominal spiracles present in the seven posterior pairs, much smaller than thoracic but quite evident, each with collar of disk pores within mouth, the posterior pair set within the chitinized area quite close to the anal opening; derm bearing small circular disk pores with circular center and about 10 loculi and slightly larger similar pores with bilocular centers and about the same number of loculi, these mostly toward posterior apex, the others well scattered; derm bearing some small setae each with stout collar and some short stiff hairs; apparently with some spines on the heavily chitinized apical

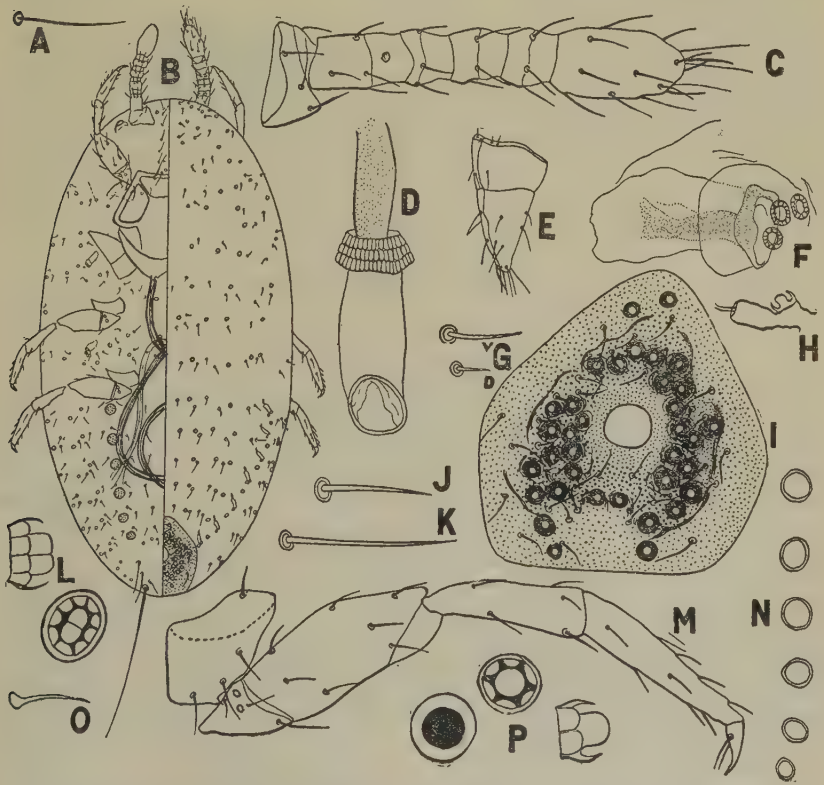

FIG. 42.—*Paracoelostoma peruviana,* larva: A, derm seta, × 430; B, outline, dorsal and ventral, × 60; C, antenna, × 230; D, anal tube, × 230; E, beak, × 120; F, thoracic spiracle, × 460; G, body setae, dorsal (D) and ventral (V), × 650; H, abdominal spiracle, × 430; I, apical chitinized disk, × 230; J, marginal seta, × 650; K, posterior ventral seta, × 650; L, spiracular disk pore, × 1,280; M, leg, × 230; N, single row of ventral cicatrices, × 120; O, ventral hair, × 650; P, derm multilocular disk pores and simple apical disk, × 1,280

plate, these greatly obscured, size and shape uncertain; anal opening apical, anal tube of moderate size, with band of wax pores at inner end, apparently without collar of disk pores at any point; ventral cicatrices numerous, varying in size, in transverse, irregular, segmental rows on both surfaces of the body.

Larva.—Decidedly elongate elliptical, posterior apex of body with a large, heavily chitinized plate surrounding anal opening, remainder of body membranous; antennae six-segmented, stout, the apical segment largest, swollen, the third shortest, much abbreviated; legs moderate in size and length, the claw slightly curved, usually with a distinct denticle, claw digitules apparently acute at apices, approaching but not attaining claw tip; beak long conical, three-segmented, the basal very narrow, with a few sensory setae at apex; thoracic spiracles fairly large, with bar and cluster of disk pores at mouth of each; abdominal spiracles in the seven posterior pairs, much smaller, but still evident, elongate tubular, each with a single disk pore immediately adjacent to opening, posterior pair not inclosed within chitinized area; derm pores of

one sort only, small with oval to obscurely bilocular center, and usually about seven loculi, these quite numerous in the chitinized plate, elsewhere scattered; derm without spines, with small setae, each with large, flat, basal collar and with a few stiff short hairs with strongly swollen bases; anal opening apical, surrounded by a chitinized plate, anal tube fairly elongate, delicate, with strong band of polygonal wax pores at inner end, but no circle of disk pores; ventral cicatrices moderate in size, each circular, in two rows, one on each side ventrally about half way between middle line and margin, normally with six in each row.

Adult male.—Not known.

This genus is based on a newly described species to which the name *peruviana* has been assigned (*136, p. 103*), collected at Saman, Piura, Peru, May 21, 1910, on zapote (*Achras sapota*) by C. H. T. Townsend (No. 228) and April 29, 1912, by E. W. Rust. The indicated distribution for the genus is therefore the Chilean subregion of the Neotropical region.

Nothing whatever is known regarding the life history or biological habits of the single included species.

Genus Cryptokermes Hempel

(Pl. 3, B, and figs. 43, 44, and 45)

First described by Hempel (*91, p. 398*) in 1900, with a single included species, *brasiliensis*, this genus was, until comparatively recently, associated with the so-called subfamily Dactylopiinae. Ferris (*49, p. 221*) in 1918 first called attention to the need for its reassignment and indicated its relationship to the series of genera here discussed, although, as will be shown below, his conclusions were not based on examples of the genotype, as he believed, but instead on specimens of a previously undescribed and only recently named species. Since the descriptive information given below differs in several details from statements made by Ferris, it seems necessary to note specifically that there are certain errors in his generic diagnosis and specific description; for example, seven pairs of abdominal spiracles are present, rather than six pairs, as stated, and very poorly developed legs and antennae are present in the adult female, instead of wholly wanting.

GENERIC CHARACTERISTICS [18]

Habit.—Inclosed within a heavy-walled test during the growing period; adult female retained within this and ovipositing therein.

Adult female.—Body nearly globular; anterior apex with a large, heavily chitinized, wrinkled and ridged patch, this inclosing the eyes and the antennae, remainder of derm membranous, the posterior apex often retaining a patch of derm and the strongly developed anal tube of the preadult stage, these attached through the retention of the preadult anal tube within that of the adult; antennae reduced to little more than small patches of setae; legs comparably reduced, poorly developed, or at most elongate conical, with well developed, distinctly multidenticulate claw and acute digitules hardly surpassing the middle of the claw; no traces of a beak; thoracic spiracles large, with broad bar and pores at opening; abdominal spiracles likewise large, but distinctly smaller than thoracic, in the seven posterior pairs, each with several disk pores in a loose band within the opening, posterior pair placed quite close to anal opening and somewhat larger; derm pores of a single type only, multi-

[18] The writer is much indebted to G. F. Ferris for an opportunity to examine partly molted specimens of the adult male of *C. mexicanus*. These are not fully satisfactory for descriptive purposes, but do show enough to strengthen the conclusions that have been advanced here regarding the relationships between these New Zealand and Neotropical genera.

locular disk, mostly with from 10 to 16 small loculi and a simple circular to somewhat oval, possibly bilocular center, these pores scattered anteriorly, but rather abundant toward posterior apex of body; derm bearing spines, these stout, each broadened at base, acute at apex, thickly distributed over the anterior chitinized area and the immediately adjacent derm; with small slender setae, these scattered, and with small hairs with strongly expanded bases, these apparently rare; anal opening apical, anal tube simple, elongate, delicate, ring at inner end very indistinctly developed, the adult tube often retaining the well developed preadult tube; ventral cicatrices wanting.

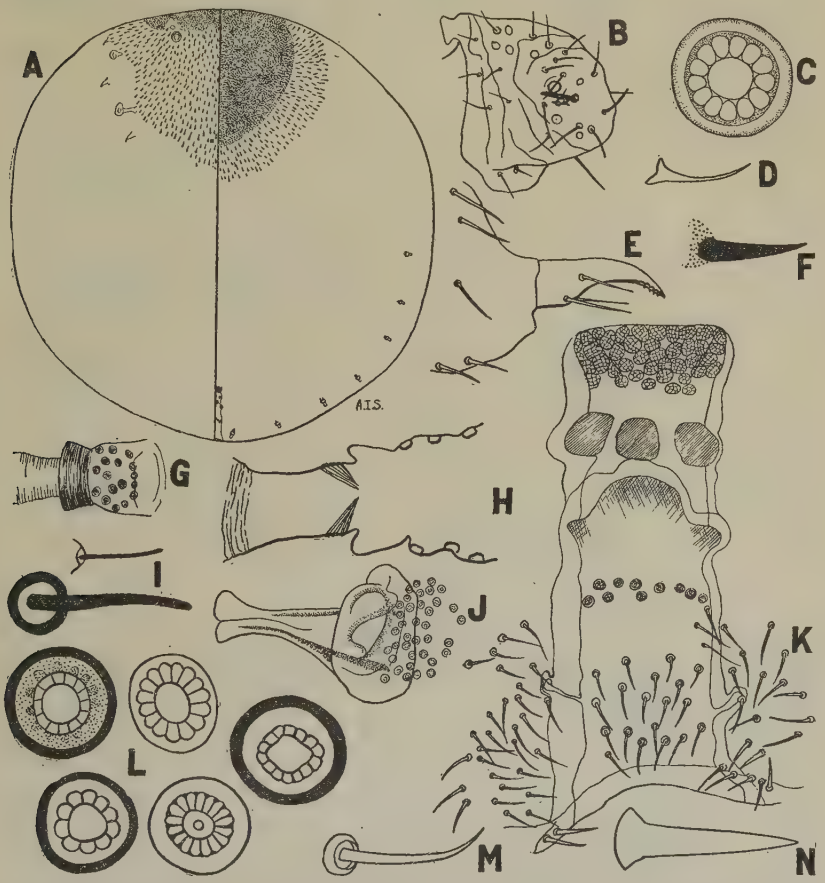

FIG. 43.—*Cryptokermes brasiliensis* (except K and N), adult female: A, outline, dorsal and ventral, somewhat diagrammatic, × 15; B, antenna, × 230; C, midventral derm pore, × 1,500; D, midventral hair, × 650; E, apex of leg, × 230; F, derm spine, × 650; G, abdominal spiracle, × 120; H, same, in section, × 230; I, derm setae, × 530; J, thoracic spiracle, × 120; K, *C. mexicanus*, anal tube, with tube of preadult still retained, × 120; L, variations in multilocular disk pores of derm, × 1,500; M, midventral seta, × 650; N, spine from head thickening of *C. mexicanus*, × 650

Intermediate female (preadult).—Approximately globular; derm mostly membranous, posterior apex, particularly toward molting time, becoming more heavily chitinized in an approximately circular area surrounding the anal opening, this area broken out in cast skins of the stage; antennae about half developed, short, tapering somewhat, apex rounded, indistinctly three-segmented to fairly distinctly six-segmented; legs likewise about half developed, or less, the segmentation more or less distinct, claw definitely developed, with denticles or irregularities, and digitules, these blunted at tips, not reaching claw apex; beak moderately elongate conical, three-segmented, the basal segment very

narrow and incomplete, with a few acutely pointed sensory setae at apex, thoracic spiracles large, with stout bar and with pore cluster at mouth, abdominal in seven pairs, distinctly smaller, but of good size, each with a loose band or circle of disk pores in and around mouth; derm pores of a single multilocular disk type, with between 10 and 16 loculi, the centers circular to

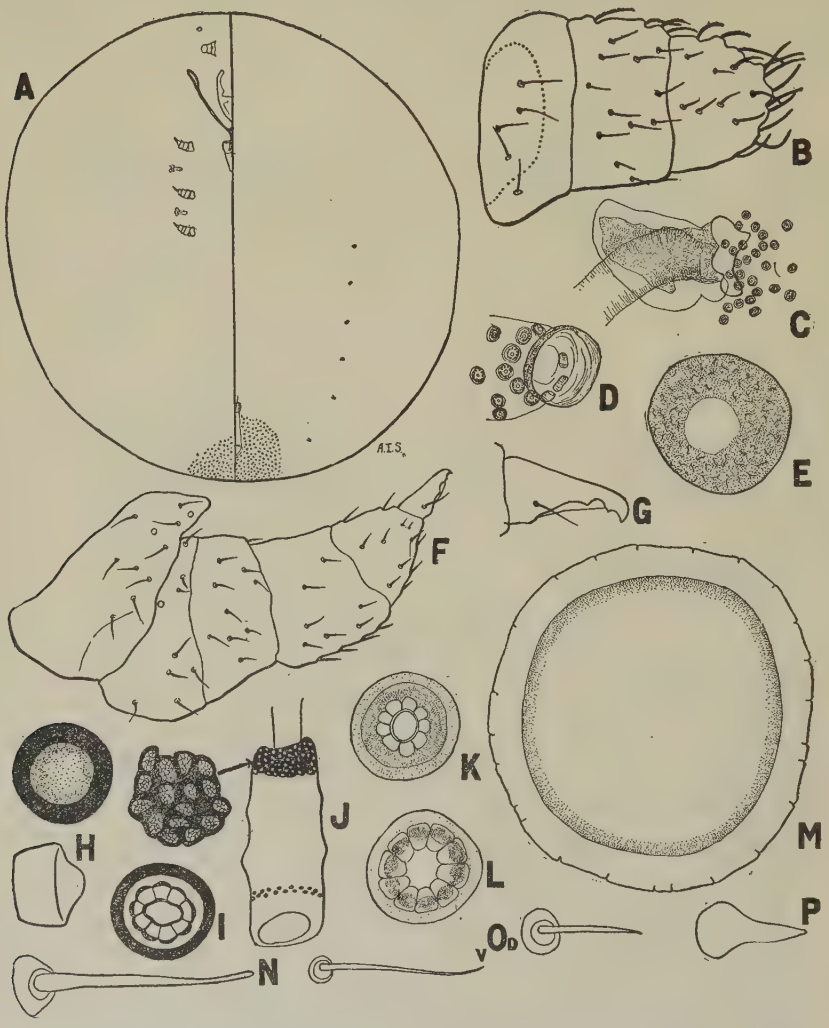

FIG. 44.—*Cryptokermes brasiliensis*, preadult female: A, outline of body, dorsal and ventral, × about 12; B, antenna, × 230; C, thoracic spiracle, × 120; D, abdominal spiracle, × 230; E, simple disk pore near posterior apex of body, × 1,500; F, leg, × 230; G, claw, × 530; H, small disklike tubercles near posterior apex of body, × 1,500; I, multilocular disk pore, × 1,500; J, anal tube, × 60, with detail, × 230; K, midventral multilocular disk pore, × 1,500; L, dorsal multilocular disk pore, × 1,500; M, single ventral cicatrix, × 1,500; N, seta from posterior apex of body, × 650; O, setae from middorsal (D) and midventral (V) regions, × 650; P, dorsal spine from posterior end of body, × 650

oval to somewhat trilocular to quadrilocular or even quinquelocular, these in general rather more abundant posteriorly; derm bearing stout conical spines, these very few to numerous, more abundant in each case posteriorly; with peculiar flattened disks, these with or without a somewhat raised and pointed central boss, quite numerous over much of body; with small, short, fairly thick setae with conical basal collars; with similar small, cylindrical hairs with

expanded bases, these apparently rare; anal opening apical, surrounded by a circular, chitinized, roughened and ridged plate, anal tube elongate, with broad band of polygonal wax pores at inner end and an irregularly double circle of disk pores somewhat nearer to opening than to inner end; ventral cicatrices small, circular, varying somewhat, fairly numerous, in irregular, transverse, segmental rows on both surfaces of the body. Antepenultimate female practically identical with the preadult, size somewhat smaller, various structures, spines, anal tube, cicatrices, etc., somewhat less developed.

Larva.—Elliptical in outline, not chitinized; antennae six-segmented, the sixth longest and largest, the third very short, bearing some sensory setae on apical segment, none of the setae extremely long as in Icerya and its relatives;

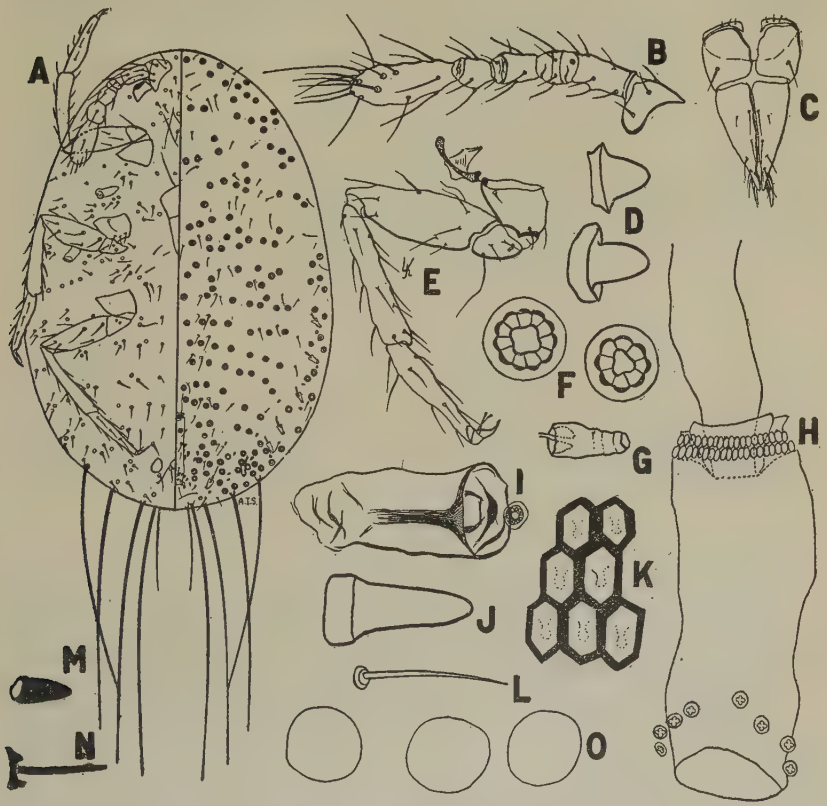

FIG. 45.—*Cryptokermes brasiliensis* (except A, H, M, N), larva: A, *C. mexicanus*, outline, dorsal and ventral, × 60; B, antenna, × 115; C, beak, × 115; D, derm disks or spines, × 1,500; E, leg, × 460; F, derm disk pores, × 1,500; G, abdominal spiracle, × 530; H, *C. mexicanus*, anal tube, × 330; I, thoracic spiracle, × 460; J, derm spine, × 1,500; K, detail of polygonal wax pores of anal tube, × 1,500; L, ventral seta, × 650; M, *C. mexicanus*, derm spine, dorsal, × 530; N, *C. mexicanus*, derm seta, × 530; O, ventral cicatrices, × 330

legs fairly long, not unusual, claw slender, curved, with distinct denticle, claw digitules slender at tips, perhaps knobbed, exceeding apex of claw; beak elongate conical, distinctly three-segmented, the basal segment merely a narrow ring, apex of beak with a few sensory setae; thoracic spiracles large, with broad bar and single disk pore directly at mouth; abdominal spiracles in seven posterior pairs, elongate tubular, with several constrictions between mouth and inner end; body with a single type of multilocular disk pore, this with trilocular to quinquelocular center and a ring of loculi outside the center, small, distributed nearly uniformly over whole body, but not numerous; derm bearing near the posterior apex of the body some stout conical spines, these tending to cluster dorsally on each side of the anal opening; also bearing tubercles, these

distributed fairly uniformly over the entire dorsum, flat, or, in one species, with elevated conical central boss, sometimes much enlarged into a strongly protruding stout spine; with, in the aggregate, a considerable number of rather stiff setae, these varying in size, larger along the body margin, and including four pairs of much longer and larger apical and subapical setae, these attaining a length of perhaps three-fifths that of the body; anal opening apical, anal tube elongate, large, with a band of polygonal wax pores at inner end, and a circle or band of multilocular disk pores around the opening; with three medium sized, circular, ventral cicatrices in a transverse row across the posterior end of the abdomen.

The present known distribution of this genus includes southern Brazil and southern Mexico, therefore the Brazilian and Mexican subregions of the Neotropical region.

There seems to be no definite information available regarding the life cycle of the species of this genus.

As previously stated, there are actually two known species in the genus. All of the published records of the occurrence of *brasiliensis* in Mexico actually relate to a previously undescribed species to which the name *mexicanus* was recently assigned (*136, p. 103*). These references include that by Cockerell (*25, p. 469*) and the one by Ferris already cited in connection with this genus (*49*).

KEYS TO SPECIES OF CRYPTOKERMES

Adult female

a. Legs relatively well developed, short conical, with a distinct claw bearing digitules ..... *brasiliensis* Hempel

aa. Legs represented merely by a cluster of setae and some wrinkling and thickening of the derm; no claw observed (based on limited and inadequate material) ..... *mexicanus* Morrison

Intermediate female

a. Stout spines relatively very rare on derm, occurring only occasionally; antennae short, rounded conical, segmentation indistinct; legs also short conical, little better developed; flattened derm tubercles with slightly elevated, pointed, central boss ..... *brasiliensis* Hempel

aa. Stout spines on derm relatively very numerous, particularly at posterior end of body; antennae somewhat longer, much better developed, quite distinctly six-segmented; legs likewise much better developed, strongly chitinized, the segments distinct; flattened derm disks with the central area plane or at most slightly convex ..... *mexicanus* Morrison

Larva

a. Derm disks each with a raised and pointed central boss, some, near posterior apex, strongly elevated to form definite, stout, spinelike protuberances. *brasiliensis* Hempel

aa. Derm disks with upper surface flattened, or, at most, slightly convex. *mexicanus* Morrison

As a point of some historical interest it may be noted that as early as 1897 the late Theodore Pergande had indicated that the Mexican species here discussed represented a then undescribed genus and species.

GENUS MIMOSICERYA COCKERELL

(Pl. 3, C, and figs. 46, 47, and 48)

This genus was first established by Cockerell (*26, p. 717; 23, p. 233*) in 1902 as a "section" of the genus Icerya. Regardless of

Cockerell's designation of its rank, it complies with the nomenclatorial requirements of a subgenus, even as defined by him, since it is in the form of a generic name and has a definitely designated type species. The present placing of the unit is some indication of the true character of its supposed relationship to Icerya. Much later Newstead (*152, p. 175*) redescribed at length the single included species, originally known as *Icerya hempeli* Cockerell, and erected still another genus, Clypeococcus Newstead, for its reception, on the ground that the insect possessed a clypeus. This structure is actually nothing more than a fold or folds in the derm anterior to the attachment of the beak in the preadult female, and, in the writer's experience, its size and appearance vary more or less with the individual

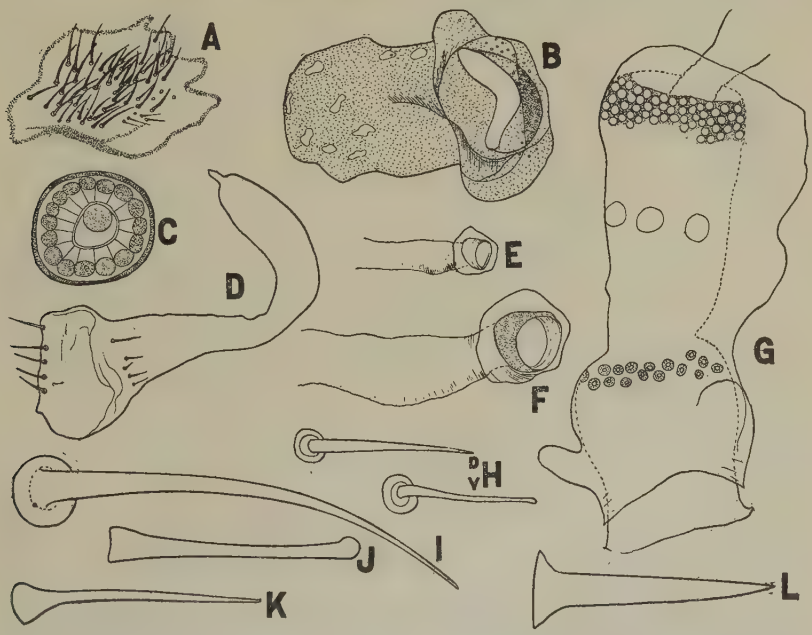

FIG. 46.—*Mimosicerya hempeli*, adult female: A, antenna, × 120; B, thoracic spiracle, × 60; C, dorsal derm disk pore, × 1,500; D, leg, × 120; E, abdominal spiracle, × 60; F, same, × 120; G, anal tube inclosing tube of preadult, × 120; H, setae, dorsal (D) and ventral (V), × 650; I, dorsal seta near apex of abdomen, × 650; J, ventral hair near leg, × 650; K, ventral hair, × 650; L, spine from cephalic plate, × 650

specimen examined. Newstead's genus therefore stands as a synonym of Mimosicerya.

In reality, as will be evident from the descriptive matter which follows, the true characteristics of this insect have never yet been made known, and its peculiar adaptation in its later stages, which, though it closely parallels that found in the preceding genera, yet differs conspicuously in certain details, is in some respects the most curious modification found within this whole group of genera.

GENERIC CHARACTERISTICS

Habit.—Remaining exposed on the host plant, but with the preadult female becoming globular and very heavily chitinized at maturity and retaining within it the adult female.

Adult female.—Shape of body probably approaching globular; derm membranous, except for a definite, heavily chitinized area at the anterior apex of the body, this practically identical with that found in Cryptokermes, and ridged and wrinkled, bearing numerous spines of varying stoutness and enclosing the eyes and the greatly reduced platelike antennae; legs elongate, slender, very slightly swollen and chitinized at tips and usually bearing a stout conical claw, but no digitules, remainder of leg membranous, joints and parts both obliterated; beak apparently wanting (one specimen examined); thoracic spiracles large, with broad bar and band of disk pores at opening; abdominal spiracles distinctly smaller, but still of considerable size, situated on truncate conical, protruding, somewhat chitinized tubercles, almost certainly in seven pairs, not accompanied by disk pores, the posterior pair close to anal opening; derm pores of a single multilocular disk type, circular to slightly oval, with centers circular or obscurely bilocular or trilocular and numerous submarginal loculi (about 15 or 16), these pores much more abundant toward the posterior apex of the body; derm, in addition to the numerous spines on the cephalic chitinized area, with large, but not dense, clusters of more slender spines around each thoracic spiracle; with some slender, but many more short stiff setae over body,

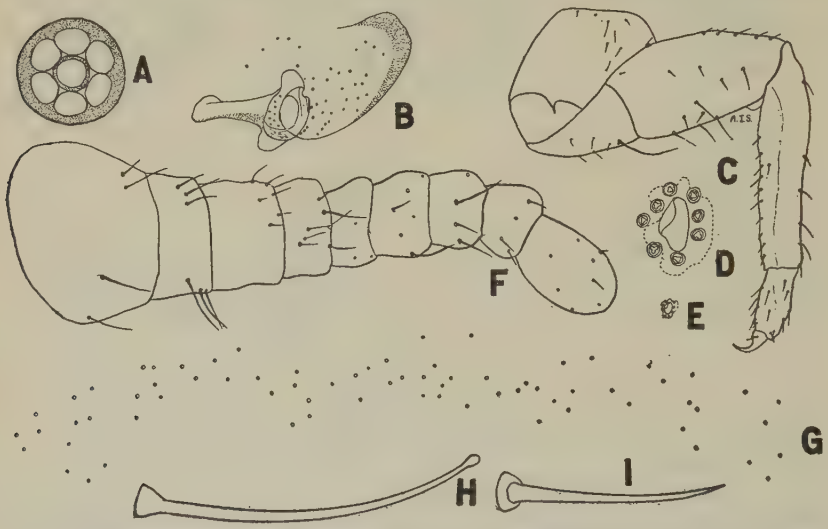

FIG. 47.—*Mimosicerya hempeli*, preadult female: A, derm disk pore, × 1,500; B, thoracic spiracle, × 60; C, leg, × 60; D, abdominal spiracle, × 230; E, same, × 60; F, antenna, × 115; G, row of ventral cicatrices, × about 40; H, ventral hair, × 650; I, ventral seta, × 650

these decidedly larger, stouter, and more abundant at posterior end; with a few stiff hairs with expanded bases scattered about, apparently promiscuously; anal tube delicate, hardly chitinized, without pores, normally retaining the tube of the preadult stage; no ventral cicatrices.

Intermediate female (fully mature preadult only).—Approximately spherical, naked, or with a faint bloom, heavily chitinized, excepting only the midventral area in contact with the host plant, posterior end with a small, roughly circular opening; antennae well developed, eight-segmented to nine-segmented; legs fully developed, short and rather stout, the parts distinct, claw stout, curved, claw digitules apparently short, slender; beak small, structure uncertain in material examined, apparently indistinctly two-segmented with very few setae; thoracic spiracles large, with bar and cluster of pores at mouth; abdominal much smaller, with disk pores in and at mouth, apparently in six pairs, actually with seven, the last pair included in the circular dermal plate attached to the anal tube retained by the adult female; derm dorsally and laterally bearing some small disk pores with about five to eight loculi and some setae, but the number and arrangement of these obscured and somewhat uncertain, midventral derm bearing some pores with quadrilocular centers; heavily chitinized margins of midventral area bearing numerous long, slender, flexible,

nearly cylindrical hairs, with expanded bases and, usually, with more or less swollen apices, these in a rather dense band around the body margin at this point and also extending over the area between and around the legs; no stout conical spines observed; anal opening apical, anal tube with a wide collar of polygonal wax pores at inner end and a double to triple row of multilocular disk pores nearer opening than inner end; ventral cicatrices numerous, small, circular, of varying size, in irregular transverse segmental rows on abdomen and thorax, extending across membranous ventral surface and into chitinized area on each side.

Larva.—Very similar to that of Cryptokermes; elliptical; the antennae elongate, only moderately stout, six-segmented, the third very short, the terminal elongate, somewhat swollen, bearing sensory setae at apex; legs slender, claw slender, slightly curved, with denticle, claw digitules slender, not exceeding

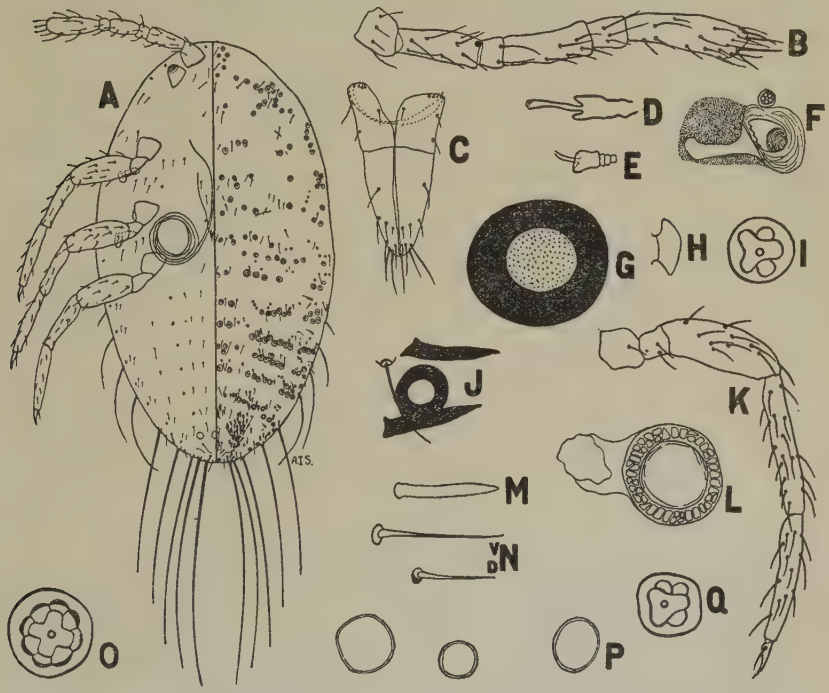

FIG. 48.—*Mimosicerya hempeli*, larva: A, outline, dorsal and ventral, × 60; B, antenna, × 120; C, beak, × 120; D, abdominal spiracle, in section, × 530; E, same, × 460; F, thoracic spiracle, × 460; G, heavy derm disk or tubercle, × 1,500; H, same, profile, × 650; I, derm disk pore, × 1,500; J, section of derm with tubercle, spines, and seta, × 530; K, leg, × about 100; L, anal tube, × 330; M, derm spine, × 650; N, derm setae, dorsal (D) and ventral (V), × 650; O, derm disk pore, × 1,500; P, ventral cicatrices, × 330; Q, abnormal derm disk pore, × 1,500

claw apex; beak elongate conical, three-segmented, the basal segment very narrow, with some acute sensory setae at apex; thoracic spiracles of moderate size, with bar and with a single pore at opening of each; abdominal spiracles in seven pairs, much smaller, but still distinct, elongate as in Cryptokermes, with a disk pore near to but not intimately associated with the opening of each; derm pores of a single disk type only, not numerous, of moderate size, with four to six loculi, those near spiracles larger; derm dorsally bearing elongate, nearly cylindrical spines, tapering to point at apices, in clusters on each side of the anal opening and in paired transverse rows anterior to the clusters, these rows dwindling to one or two spines on each margin within three or four segments; with numerous flat toadstool-shaped tubercles, larger and more numerous posteriorly, distributed in transverse rows over the whole dorsum; with slender setae, having stout conical bases and, at the posterior

apex of the body, five pairs of much larger setae, these attaining a length as much as three-fifths that of the body; anal opening apical (appearing subapical in many mounted specimens), short, with a double collar of polygonal wax pores at inner end, but no ring of disk pores; with three circular ventral cicatrices of moderate size, in a transverse row beneath anal tube.

Adult male.—Not known.

The present known distribution of this genus is that of its single member and includes southern Brazil only.

There appears to be no information published in regard to its biology.

As indicated by the details of the generic description, this genus is, on morphological characters, very closely related to Cryptokermes. It is at present considered that the peculiar modifications described

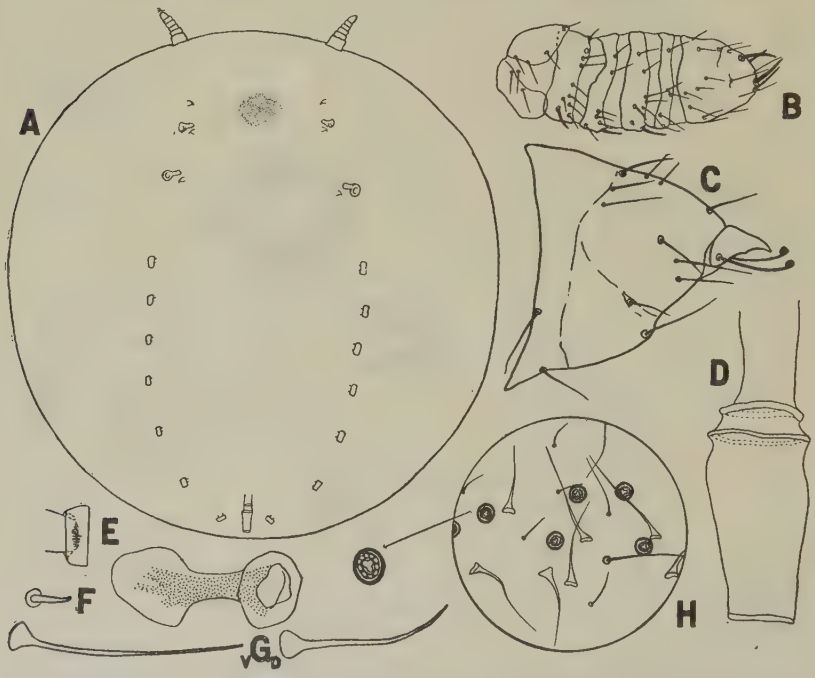

FIG. 49.—*Ultracoelostoma assimile*, adult female: A, outline, optical section, × 12; B, antenna, × 165; C, middle leg, × 440; D, anal tube, × 165; E, left, abdominal, and right, thoracic spiracle, × 165; F, dorsal seta, × 650; G, ventral (V) and dorsal (D) hairs, × 650; H, section of derm, × 165

for the preadult and adult stages are adequate to justify the acceptance of separate generic status for the single included species.

GENUS ULTRACOELOSTOMA COCKERELL

(Pl. 3, D, and figs. 49, 50, 51, and 52)

This genus was established by Cockerell (*21, v. 35, p. 114; 23, p. 258*) in 1902 to receive the species described by Maskell as *Coelostoma assimile*. The genus and its single included species have been discussed at some length recently (*137, p. 11*). Although there seemed to be some doubt as to the correctness of Maskell's identification of the adult female when the species was first studied, a later examina-

tion of the available specimens of this stage leads to the belief that, on morphological grounds alone, the stage can be considered as having been correctly determined by him.

GENERIC CHARACTERISTICS

Habit.—Inclosed during the growing period within a hard, apparently somewhat calcareous test, often located in the axils of the host twigs and often inducing some gall formation; adult female retained within, and ovipositing in, the test of the preceding stage.

Adult female.—Nearly globular, membranous, except for a somewhat chitinized, wrinkled and ridged, platelike area on the apex of the head; antennae much reduced, stout, tapering, more or less distinctly five-segmented to seven-

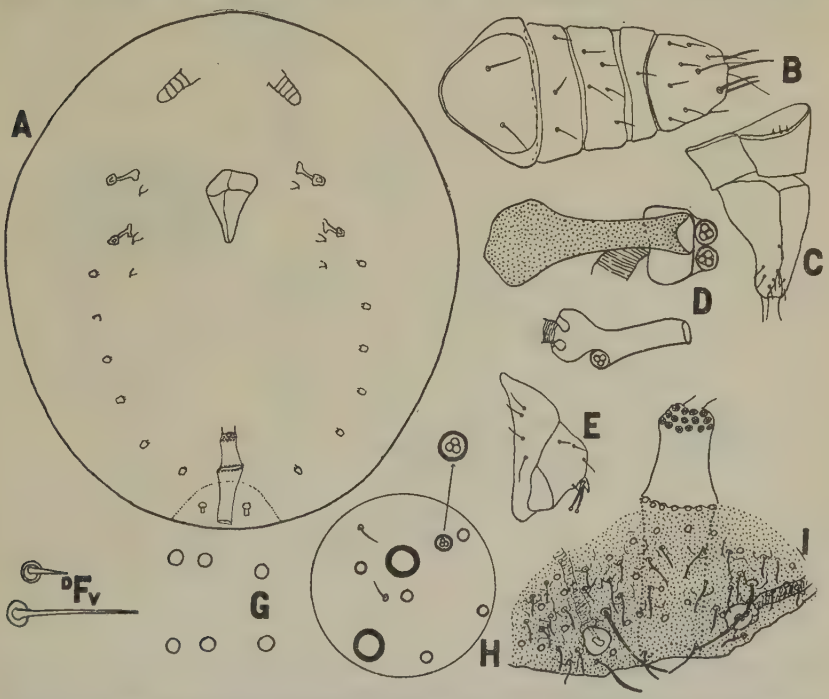

FIG. 50.—*Ultracoelostoma assimile,* preadult female (except I, this second-stage female): A, outline, × 60; B, antenna, × 335; C, beak, × 120; D, thoracic and abdominal spiracles, × 500; E, leg, × 335; F, dorsal (D) and ventral (V) setae, × 650; G, ventral cicatrices, × 165; H, section of ventral derm, × 335, with detail of pore, × 640; I, apex of abdomen, × 165

segmented; legs reduced to stout cones, each bearing a somewhat curved claw at the end, this often with a denticle, and two, or sometimes three, slender digitules distinctly knobbed at apices, leg with a few setae, segmentation practically wholly obscured; beak wanting; thoracic spiracles of moderate size, with slender bar and row of disk pores at mouth; abdominal spiracles in seven posterior pairs, conspicuous, openings approaching those of thoracic spiracles in size, without pores within atrium, but with a vague scattered cluster of disk pores around mouth, posterior pair quite close to anal opening, somewhat larger and sometimes less heavily chitinized than with the remainder; derm pores few, scattered, most numerous on the posterior abdominal segments, of one sort, multilocular disk, with about nine to eleven loculi and nearly circular, oval or triangular or almost trilobate centers; derm with a few small, inconspicuous setae with flat basal collars; with slender delicate hairs with strongly expanded hemispherical bases, these sparse on anterior portion of body, becoming much more numerous and abundant at the posterior apex; no spines or

comparable structures; anal opening apical, inconspicuous, anal tube very delicate, with a somewhat chitinized ring at inner end and a short constricted continuation of the tube; no ventral cicatrices.

Intermediate female.—Form nearly globular, derm membranous, except for a heavily chitinized circular plate at the posterior apex of the body, centered on the anal opening and including the posterior pair of spiracles within its limits; antennae much reduced, poorly four-segmented to five-segmented, with some apical sensory setae; legs even more reduced than in adult, but retaining claw, knobbed digitules, and some of the setae; beak long and sharply conical, three-segmented, the basal a very narrow collar, with about six apical sensory setae; thoracic spiracles of moderate size, with bar; abdominal nearly as large, with cylindrical entrance passage having a disk pore or pore collar at inner end, these spiracles approximately submarginal dorsal, the posterior, as stated, associated with the posterior dermal plate; derm pores apparently of one sort only, small flat disk pores, with large, usually quadrilocular but often trilocular or quinquelocular centers and no apparent small loculi, these numerous, but never crowded, distributed over the whole surface, more abundant toward the

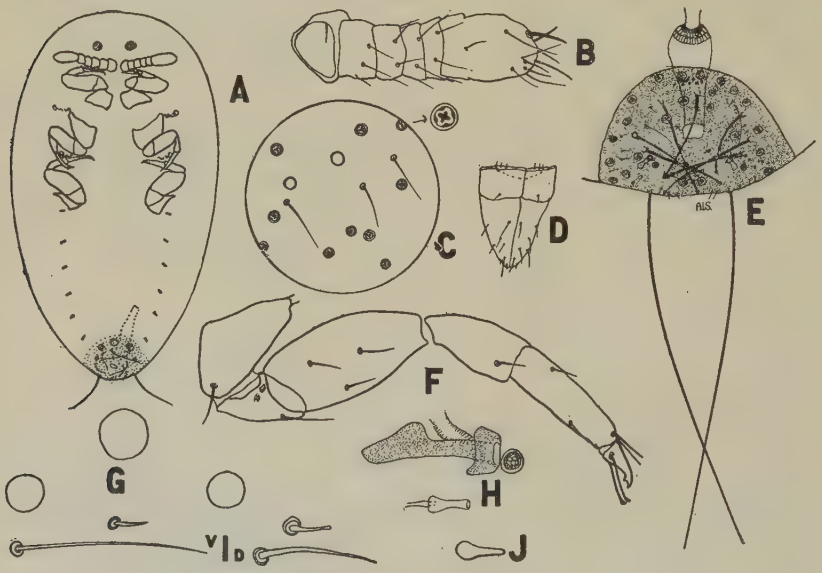

FIG. 51.—*Ultracoelostoma assimile*, larva: A, outline, optical section, × 57.5; B, antenna, × 220; C, section of ventral derm between legs, × 335, with pore detail, × 640; D, beak, × 115; E, apex of abdomen, × 165; F, leg, × 220; G, ventral cicatrices, × 330; H, thoracic and abdominal spiracles, × 460; I, ventral (V) and dorsal (D) setae, × 650; J, derm spine, × 650

posterior apex; derm with even more numerous small, flat, cylindrical tubercles, about equal in diameter to the pores, these distributed nearly uniformly; derm with some small setae with flattened collars; with some hairs, these short, nearly cylindrical, with rounded tips and strongly expanded bases, distinctly stouter than the setae; anal opening apical, in the center of a chitinized, circular, ridged and roughened plate, anal tube long, with a band of polygonal wax pores at inner end and a single circle of multilocular disk pores about one-third the total length from the inner end; ventral cicatrices fairly numerous, in paired, transverse, irregular clusters on the intermediate abdominal segments.

Larva.—As mounted, stout elliptical; derm membranous except for a distinctly chitinized circular plate surrounding the anal opening; antennae six-segmented, short and stout, the sixth much the longest and largest, with several stouter sensory setae at apex; legs short, moderately stout, claw curved, with a very distinct denticle, claw digitules slender, distinctly knobbed, surpassing claw apex; beak rather elongate conical, three-segmented, the basal a very narrow, incomplete collar, apex with a few acute sensory setae; thoracic spiracles of moderate size, with bar and pore at mouth; abdominal spiracles in

the seven posterior pairs, distinctly smaller but still of considerable size, the entrance tube elongate, cylindrical, expanded at inner end, the posterior pair distinctly enlarged, situated close to the anal opening within the chitinized apical plate; derm pores fairly numerous, apparently of only a single sort, small quadrilocular disk, these distributed rather uniformly over dorsal surface at least; derm with small flattened tubercles comparable to those of preadult, these also well distributed; with some small, inconspicuous body setae; with a few even shorter, but stouter, hairs, with strongly expanded bases; with a single pair of apical setae, about one-fourth that of the body in length; apical plate bearing several elongate setae having slightly clavate, rounded apices; anal tube delicate, opening in center of apical chitinized plate, with a double band of polygonal wax pores at inner end and a circle of disk pores about one-third

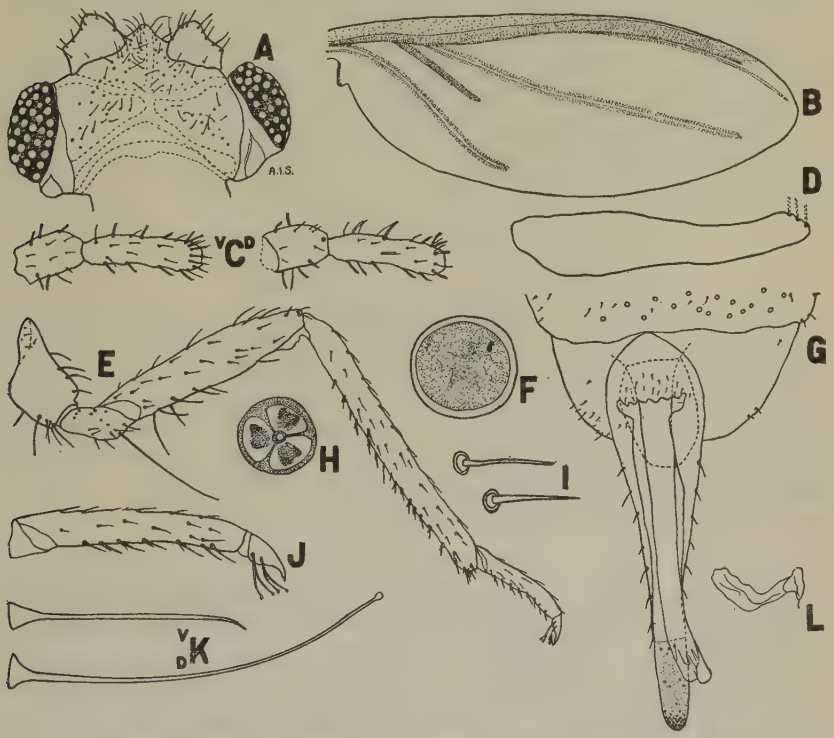

FIG. 52.—*Ultracoelostoma assimile,* adult male (from specimens determined by G. Brittin): A, head, dorsal, × 60; B, wing, × 17.5; C, antenna, second and third segments, dorsal and ventral, × 60; D, halter, with apical setae incomplete, × 120; E, leg, × 60; F, ventral tubercular disklike pore, × 1,500; G, apex of abdomen, ventral, × 120; H, derm disk pore, × 1,500; I, derm setae, × 650; J, tarsus and claw, × 120; K, derm hairs, dorsal (D) and ventral (V), × 650; L, abdominal spiracle, × 530

of total length from base; with three circular ventral cicatrices, placed beneath chitinized plate, the two laterals posterior to the median.

Adult male (from specimens determined by G. Brittin).—Of the usual elongate shape; head apex and antennae as in Coelostomidia, the segments beyond the second elongate, nearly cylindrical, without nodes or whorls of setae; legs rather elongate, the tibia bearing some bifurcate setae, the tarsus distinctly two-segmented, claw slender, strongly curved, with distinct denticle, digitules slender, strongly knobbed at apices, exceeding claw tip, each claw with two pairs; wing as in Coelostomidia, rather narrow, only slightly cloudy, the costal complex continued faintly as a darker streak beyond the normal termination to the wing apex, basal diagonal vein very short; halteres uncertain, apparently narrow as in Coelostomidia; abdomen membranous, without traces of thickened darker patches, and with no sort of suggestion of apical or other lobes or

tassels; penis sheath very elongate conical, tapering uniformly from base to apex, this last rounded; abdomen with small, flattened, cylindrical tubercles in bands beneath as in Coelostomidia; with the usual disk pores dorsally, these mostly trilocular, and with small setae in more or less distinct transverse bands dorsally, elsewhere scattered.

The genus, as at present accepted, is found only in New Zealand.

No definite information regarding the biology of the single included species seems to be available. The habit, including the formation of the heavy protective test by the immature stages of the female, and the continued inclosure of the adult female within this test, together with the reduction in the legs and antennae of this stage, are noteworthy. Perhaps it may be noted here that a critical investigation of this species in New Zealand is desirable. Certain of the various lots of material examined in connection with this study show some differences, when compared with the Maskell type material, that hint at specific distinctness, such as, in the adult female, for example, larger size, and the presence of three knobbed digitules on the claw, the latter in contrast to the two pairs present in type specimens.

Genus Coelostomidia Cockerell

(Pl. 3, E, and figs. 53, 54, 55, and 56)

This genus was first erected by Maskell (*122, p. 294*) in 1880 as Coelostoma, with the single included species *zealandica* Maskell. Much later Cockerell (*20, p. 367*) substituted for Maskell's generic name the name Coelostomidia, as the name first proposed was shown to be preoccupied. In addition to various notes by Maskell and other writers, the structural characters of the species have recently been discussed at some length (*137, p. 7*). Much of the matter included here has been obtained from this last paper cited.

GENERIC CHARACTERISTICS

Habit.—Inclosed during the growing period within a globular, thick-walled, presumably secreted protective cell; adult female free, active, secreting a mass of cottony material at oviposition.

Adult female.—Body somewhat elongate ovoid as mounted, derm remaining membranous; antennae fully developed, 11-segmented, stout, tapering somewhat, the segments short and the intermediate ones broader than long, some of the segments with sharply differentiated sensory setae; legs large, stout; the setae on under side from long and slender to stout, almost spinelike in certain species, claw stout, curved, sometimes roughened or faintly denticulate near tip, digitules approaching claw apex, slender, faintly knobbed at tips; beak perhaps usually wanting, but sometimes developed, when absent the derm in the area usually bearing it folded and somewhat thickened, no definite indication of full development of internal framework and the setalike mouth parts in any specimens, beak, where present, moderately elongate conical, obscurely two-segmented, apex with a few pointed sensory setae; thoracic spiracles of moderate size in relation to the body dimensions, with bar and a small pore cluster at mouth; abdominal spiracles in the seven posterior pairs, large, not conspicuously smaller than thoracic, with or without a few disk pores within atrium, but without any definite collar of pores, apical pair of spiracles placed immediately adjacent to the anal opening; derm pores of one type only, multilocular disk, circular to oval, with from 8 to 11 loculi and the centers circular to elongate elliptical, or often more or less distinctly bilocular or trilocular; derm without spines; with numerous mostly small to moderately long slender hairs, with broadened bases tapering gradually to apices, or with more or less flat conical bases; derm setae likewise small and slender, with stout conical bases, mostly hardly larger than the hairs, some along margin

larger, but not conspicuously so; anal tube rather large and long, opening at the posterior apex of the body, delicate, with a somewhat chitinized ring at the inner end; ventral cicatrices wanting.

Intermediate female (preadult).—Body approaching a globular form, or at least very broadly elliptical, membranous or with posterior end more or less heavily chitinized; antennae very short and stout conical, strongly reduced, apex rounded, bearing some specialized sensory setae, segmentation somewhat indistinct, but with about eight or nine segments in fully chitinized antennae;

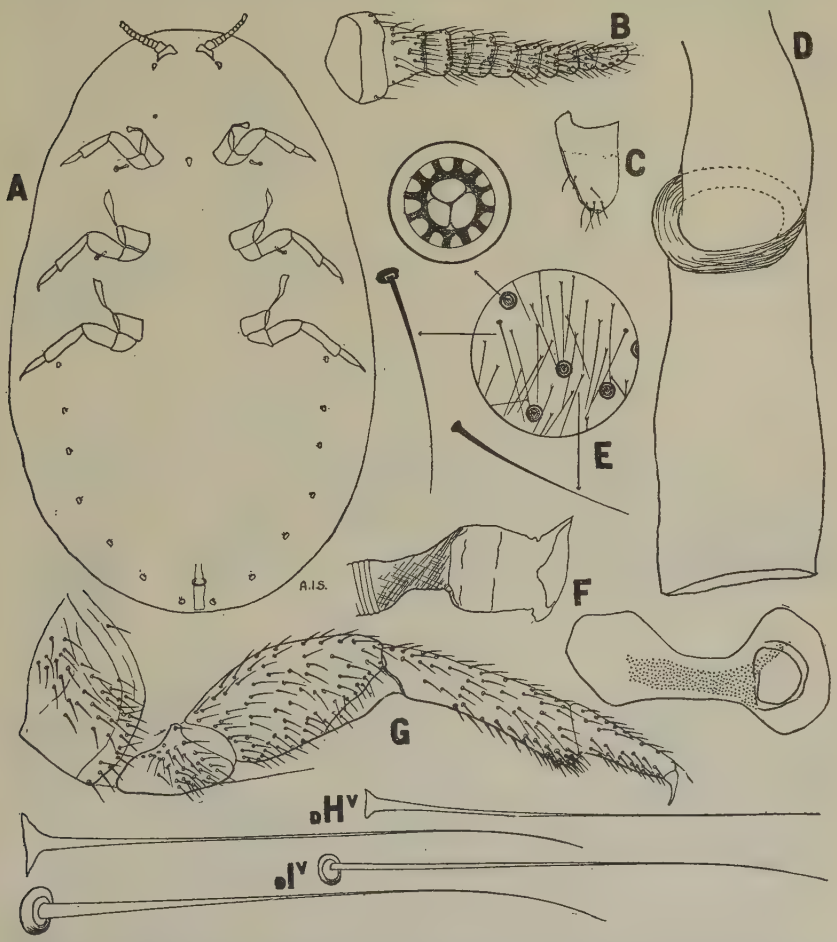

FIG. 53.—*Coelostomidia zealandica*, adult female: A, outline, optical section, × 7.5; B, antenna, × 30; C, beak, × 165; D, anal tube, × 115; E, section of derm, × 165, with details of setae, × 335, and of disk pore, × 1,500; F, abdominal and thoracic spiracles, × 115; G, leg, × 30; H, dorsal (D) and ventral (V) hairs, × 650; I, dorsal (D) and ventral (V) setae, × 650

legs much reduced, approximately triangular in outline, the segments indistinctly indicated by lighter cross lines representing joints, claw developed but small, often with denticle, claw digitules approaching tip of claw; beak moderately but rather sharply elongate conical, distinctly two-segmented, perhaps even three-segmented, with a very narrow basal collar, apex with a few stouter sensory setae; thoracic spiracles of moderate size, with bar and a small cluster of pores at opening; abdominal spiracles in the seven posterior pairs, the opening a little smaller than that of thoracic, atrium of each with a more or less

developed collar of disk pores at inner end, the posterior pair quite close to anal opening; derm pores of two sorts, multilocular disk, showing some variation in appearance, and, more numerous, trilocular, or, rarely, quadrilocular-center disk pores with, usually, three accessory loculi, these last pores scattered over body; derm with spines, these taking on the characteristic form of spines or reduced to mere short conical or even hemispherical tubercles, more or less numerous (very numerous in the species with spines); derm hairs rather short and stout with strongly expanded bases, tips tapering, or slightly swollen; anal opening apical, sometimes surrounded by a somewhat chitinized plate, the tube long, with a broad band of polygonal wax pores at inner end and

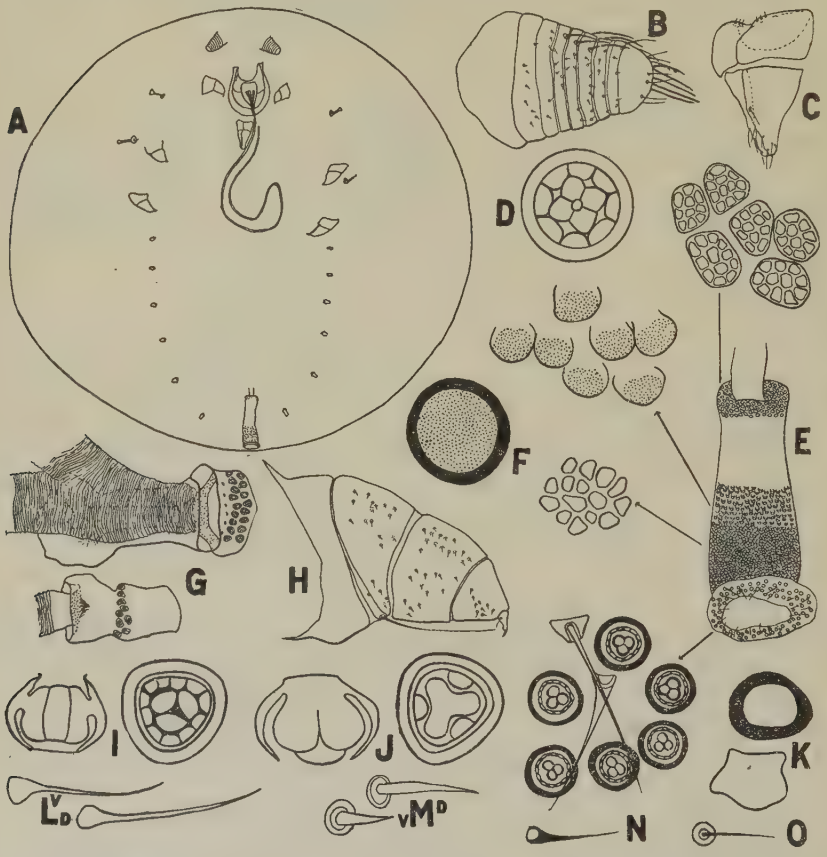

FIG. 54.—*Coelostomidia zealandica*, preadult female: A, outline, optical section, × 12; B, antenna, × 115; C, beak, × 60; D, derm pore, × 1,500; E, anal tube, × 57.5, with details, × 640; F, ventral cicatrix, × 640; G, thoracic and abdominal spiracles, × 165; H, middle leg, × 165; I, derm pore, × 1,500; J, derm pore, × 1,500; K, simple derm disk, × 1,500; L, ventral (v) and dorsal (D) hairs, × 650; M, dorsal (D) and ventral (v) setae, × 650; N, derm hair, × 335; O, derm seta, × 335

a double or wider band of small, deep, multilocular disk pores beyond middle, also with multilocular disk pores around opening in a more or less definite cluster or band; ventral cicatrices varying in size, all small, numerous, in transverse, irregular, segmental rows or bands across the ventral abdominal region. (Immature female resembling the stage just described in general characteristics but less developed. It is this stage which was recently described (*138, p. 38*) and figured in some detail for the species *pilosior*, and not the older one.)

Larva (based on genotype only).—Body somewhat elongate elliptical, derm membranous to somewhat chitinized at the posterior apex around the anal opening; antennae short and stout, six-segmented, the apical segment much the

longest, somewhat enlarged, bearing enlarged sensory setae; legs of moderate length and size, claw the same, somewhat curved, with a distinct to prominent denticle, claw digitules exceeding apex of claw, knobbed at tips; beak rather long conical, incompletely three-segmented, only the anterior portion of the narrow basal segment formed, with a few acute apical sensory setae; thoracic spiracles of moderate size, with bar and disk pore or pores at mouth; abdominal spiracles in seven pairs, definitely smaller than thoracic, but conspicuous, owing to intimate association of one or two disk pores with each spiracle, the posterior pair placed close to the anal opening and distinctly larger than the remainder; derm pores varying somewhat in size, of the usual circular disk type, mostly with quadrilocular center, this sometimes with from three to six loculi, the pore with an outer band of numerous smaller loculi, or this last often apparently lacking (perhaps only very faintly developed); these derm pores fairly abundant over whole body in more or less definite transverse rows, more abundant toward caudal end; derm bearing a few hemispherical tubercles toward caudal end of body, with short conical, rather stout to elongate slender hairs,

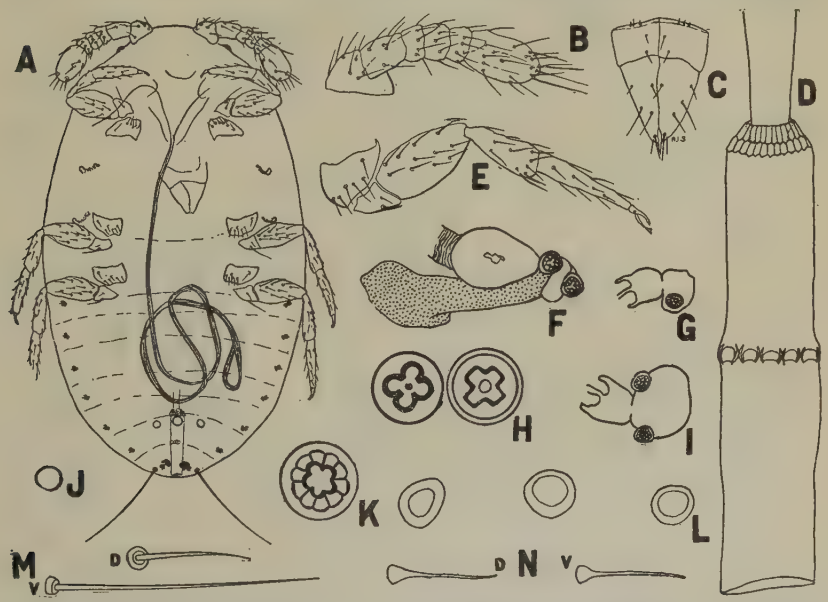

FIG. 55.—*Coelostomidia zealandica*, larva: A, outline, optical section, × 57.5; B, antenna, × 115; C, beak, × 115; D, anal tube, × 330; E, leg, × 115; F, thoracic spiracle, × 500; G, anterior abdominal spiracle, × 500; H, derm disk pores, × 1,500; I, posterior abdominal spiracle, × 500; J, simple derm disk, × 640; K, derm disk pore, × 1,500; L, ventral cicatrices, × 330; M, dorsal (D) and ventral (V) setae, × 650; N, dorsal (D) and ventral (V) hairs, × 650

each with expanded base; with slender setae, small, but varying more or less in length, and with very flat basal collar, with a single pair of enlarged apical setae, about one-fourth the body length; anal opening apical, the tube chitinized, inner end with a double collar of polygonal wax pores; with three distinct circular ventral cicatrices in transverse row before anal tube.

Adult male (based on specimens of genotype as determined by G. Brittin).—Of the usual elongate shape, general appearance and many details of structure strongly resembling the condition in Monophlebinae; apex of head flat triangular in outline; antennae elongate, slender, but distinctly shorter than body, each segment beyond second very slightly clavate, the setae fairly numerous, not arranged in any definite whorls or other sequence, terminal segment approximating preceding in length; thorax with a definite elliptical to quadrate, transverse, unchitinized area dorsally; legs moderately stout, the tibia and tarsus with numerous bifurcate setae, these wanting on anterior femora, tarsus distinctly two-segmented, claw slender to stout, with or without denticle, with knobbed digitules, these two to many (to 24) in number; wing narrow, the

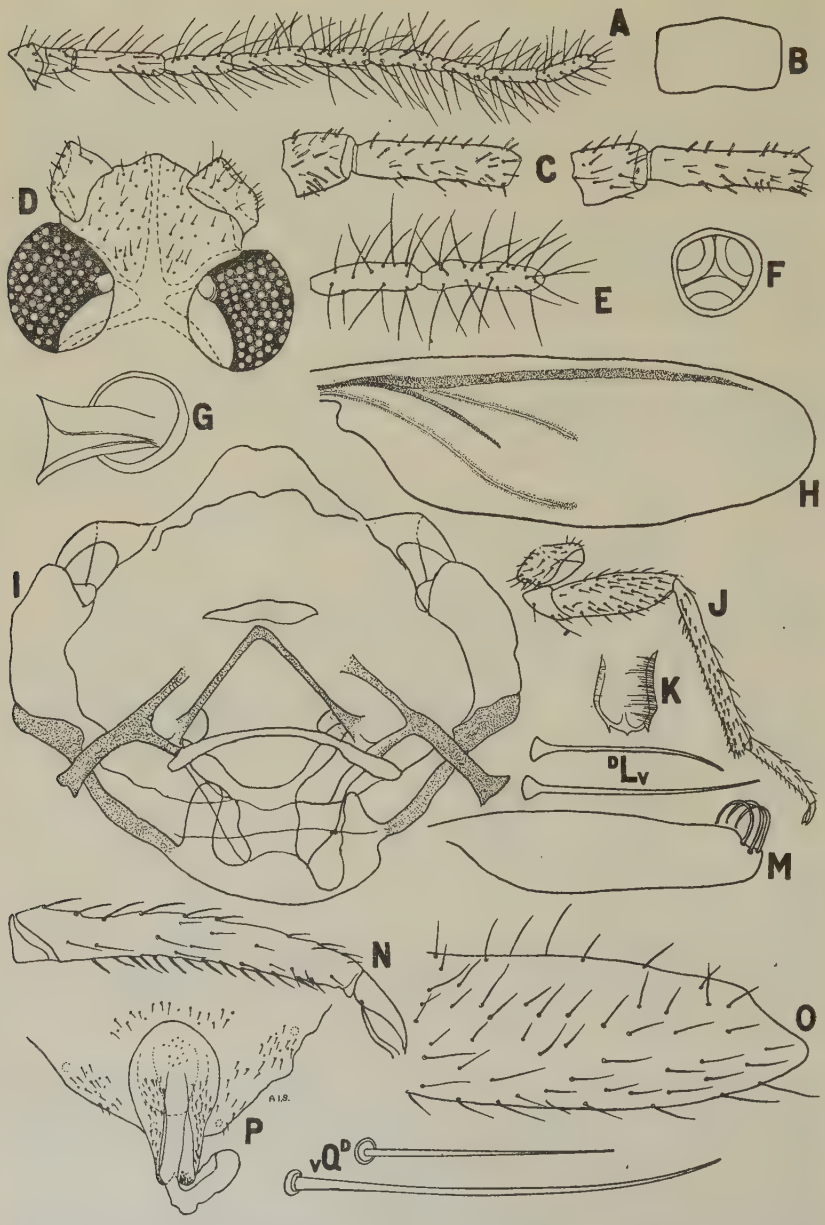

FIG. 56.—*Coelostomidia zealandica*, adult male (from specimens determined by G. Brittin): A, antenna, × 30; B, transverse clear area in dorsal midthoracic region, × 60; C, antenna, second and third segments, dorsal and ventral, × 60; D, head, × 60; E, antenna, apical and preapical segments, × 60; F, derm disk pore, × 1,500; G, abdominal spiracle, × 650; H, wing, × 17.5; I, thoracic region, somewhat distorted, × 30; J, leg, × 30; K, ventral abdominal tubercle, × 1,500; L, derm hairs, dorsal (D) and ventral (V), × 650; M, halter, × 120; N, tarsus and claw, × 120; O, apex of anterior femur, × 120; P, apex of abdomen, ventral, × 60; Q, abdominal setae, dorsal (D) and ventral (V), × 650

venation as in Monophlebinae but fainter, the diagonal vein very short, wing only slightly dusky, not strongly infuscated; halteres narrow, with three to four curved, knobbed setae at apex of each; abdomen membranous, without traces of darker markings, and with no suggestion whatever of apical or marginal lobes or fleshy tassels; penis sheath broadened and rounded anteriorily, tapering posteriorly to a broadened bilobate or even bifurcate apex, the fleshy, spine-bearing penis very elongate, nearly reaching the thorax when retracted within the body; with seven pairs of distinct abdominal spiracles, each with a ringlike collar at opening; abdomen with the usual large quadrilocular (or very often trilocular) disk pores, these not abundant, ventrally with transverse clusters of small, nearly cylindrical tubercles, of uncertain detailed structure and function, across each abdominal segment anterior to the penis sheath; derm bearing only slender, not particularly elongate setae.

This genus is known to occur only in New Zealand.

No precise information regarding the biology of the included species seems ever to have been published, although some suggestions as to feeding and oviposition habits have been given by Maskell in his various papers. The length of the life cycle can hardly be surmized from the information available.

Three species are at present included in this genus, these being *pilosa* (Maskell), *wairoensis* (Maskell), and the genotype *zealandica* (Maskell). Only the adult and immature male stages are known for the second species, and though no males of *pilosa* have been available for study, the adult male of this, according to Maskell, is very close to the male of the genotype.

The known stages of the three species may be separated by the following keys:

KEYS TO SPECIES OF COELOSTOMIDIA

Adult female

a. With relatively few (perhaps 18) stout setae on ventral face of tibia. *pilosa* (Maskell)

aa. With numerous stout setae (50 or more) on ventral face of tibia. *zealandica* (Maskell)

Intermediate female

a. Collar of multilocular disk pores about middle of anal tube several pores wide; derm without long, slender, conspicuous spines. *zealandica* (Maskell)

aa. With a single row of multilocular disk pores forming the collar about the middle of the anal tube; derm with numerous large, slender, conspicuous spines ..... *pilosa* (Maskell)

Adult male

a. With two slender, knobbed claw digitules ..... *zealandica* (Maskell)

aa. With numerous (as many as 24) slender, knobbed claw digitules. *wairoensis* (Maskell)[19]

SUBFAMILY MONOPHLEBINAE MASKELL

Although this group of genera appears to have been first outlined in a general way by Signoret (*158, p. 350*), its first definite designation as a subfamily that has come to the writer's attention is that of

[19] Numerous adult and immature male specimens of this have recently been made available through J. G. Myers. A comparison of these with the corresponding stage of *zealandica* shows close relationship except in the claw structure, and in details of shape of penis sheath in the adult male stage. Pending the acquisition of further knowledge it seems legitimate to keep these two together.

Maskell (*127, p. 28*) in 1895. Its use was subsequently restricted by Cockerell (*17, p. 273*) to practically the same limits as in this bulletin. The subfamily and many of the included species have recently been treated extensively by Vayssière (*170*).

SUBFAMILY CHARACTERISTICS

Habit.—Living unprotected or protected only by waxy secreted matter on the host branches and leaves; reproductive habit various, oviposition occurring directly beneath body, in a loose mass of cottony secretion, in a definite posterior ovisac, or within an internal marsupium having a ventral opening.

Adult female.—Body short to elongate elliptical or ovoid; derm membranous or more or less chitinized, not with particularly definite chitinized areas; antennae 7-segmented to 11-segmented, well developed, stout sensory setae differentiated or not, second segment with a single sensory pore; legs mostly rather stout, claw without definite subapical or other denticle, digitules acute, or at most somewhat blunted at apices, not attaining tip of claw, femora and often the other parts frequently, but not always, with the setae on the under side very stout, distinctly spinelike; beak very short and stout conical, one-segmented, to elongate conical, distinctly three-segmented, with the apical sensory setae acute, or bluntly rounded, or truncate, or expanded, or broadened and somewhat bifid at tips; thoracic spiracles large, with bar, with or without a cluster of disk pores on derm just outside of opening, but without pores within atrium; abdominal spiracles conspicuously smaller, with from two to seven pairs developed, these in each case the posterior pairs, and with or, more often, without one or more disk pores within atrium; derm pores mostly of the multilocular disk type, but showing decided variety in internal organization, extent of chitinization, and size, sometimes with large tubular bilocular or trilocular pores in addition to the usual flat type; derm vestiture usually dense or at least abundant, rarely rather sparse, spines present or wanting, hairs present, in some genera very numerous, in some few, and setae present, varying much in numbers, size, stoutness, color, and so on, with the genus, or even with the species; anal tube always definitely developed, always definitely dorsal in position, although sometimes fairly near posterior apex of abdomen, always with ring formed at inner end, this sometimes simple, chitinized, sometimes made up of polygonal wax pores; ventral cicatrices always present (one species uncertain, a possible exception), number varying from a single large circular one to a great many (into the hundreds).

Intermediate female.—In general resembling the adult female fairly closely; usually with fewer antennal segments, fewer pores, setae, spines, and so on; with smaller bodies, and no special developments related to reproductive activity such as an ovisac band or a marsupium; rarely with some structures, the derm spines, for example, much better developed and more conspicuous than in the adult stage.

Larva.—As mounted, elongate or normally elliptical, or ovoid, broader anteriorly; derm membranous; antennae mostly slender to moderately stout, often bearing very elongate setae, either five-segmented or six-segmented, the apical segment longest, the third usually next in length, sensory setae on apical segment differentiated or not; legs normally developed, trochanter usually with two sensory pores on each face, claw with or without denticle, claw digitules acute, blunted, or more or less distinctly knobbed, not attaining claw apex to approximating it or somewhat exceeding it; beak stout conical, one-segmented, to elongate conical, three-segmented, apical sensory setae acute to bluntly rounded, to truncate, to expanded, to almost bifid at apices; spiracles as in adult, the difference in size between thoracic and abdominal usually even more pronounced; derm pores mostly of the multilocular disk type, internal organization, extent of chitinization, and depth varying markedly, sometimes in addition with marginal rows of much enlarged deep bilocular or trilocular tubular pores that produce stout glassy threads; derm vestiture usually rather dense, spines present or wanting, hairs present, sometimes very numerous, more often very sparse, setae present, usually at least fairly numerous, varying much in size, with at least one and often more pairs enlarged to very greatly enlarged to form sets of apical setae at the end of the abdomen, and often with additional marginal setae on abdomen, or on whole body, equally, or at least conspicuously, enlarged as well; anal opening dorsal, or at

most subapical, tube definitely developed, always with ring, usually with polygonal wax pores at inner end; with one to several ventral cicatrices, these, where more than one, in a transverse curved row, or in a row forming a half oval (uncertain, possibly wanting in one species).

Adult male.—Of the usual elongate shape; apex of head rounded triangular between the antennal bases; antennae 10-segmented, segments beyond second either cylindrical and usually irregularly nodulose or, much more often, binodose or trinodose, with the longer setae arranged, respectively, in two or three whorls; legs mostly slender to moderately stout, all of the tibiae and usually the anterior femora bearing quite conspicuous bifurcate setae, these sometimes very few or, rarely, wholly lacking on femora, claw without denticle, claw digitules not distinctly knobbed, usually acute and not attaining claw apex, or, rarely, approximating it; wings varying appreciably in size and shape, mostly heavily to very heavily infuscated, the costal complex always truncated well before the apex of the wing, no apical diagonal vein, the basal diagonal short or long and approaching the wing margin, with two diagonal clear streaks always distinctly developed; halteres well developed, usually of a moderate width, with two to five or more elongate, curved, knobbed setae at tip of each; abdomen membranous or with irregular chitinized patches, with at least one, and often with several, short to very long fleshy tassels at apex and along sides; penis sheath entire or cleft at apex, broad at base, tapering strongly or gradually, ventral valve always distinctly shorter than sheath proper; abdomen always with flat disk pores, these trilocular to quinquelocular, but usually quadrilocular.

The geographical distribution of this subfamily is very wide. It is safe to state that, either through natural distribution or through dissemination by man, one or more representatives of the group are to be found in every subdivision of every one of the six major geographical regions.

The life cycles of several of the included forms have been fairly well worked out, with the result that, with a few possible exceptions, it is proper to state that under anything approximating normal conditions at least one generation is produced annually, with additional generations up to three for some species, under optimum conditions.

Five tribes, three of which have just been erected as new, have been included in the subfamily. They may be separated fairly satisfactorily by the following keys:

KEYS TO TRIBES OF MONOPHLEBINAE

Adult Female

a. Abdominal spiracles with a conspicuous row or band of disk pores in atrium immediately within opening.

b. Antennae normally seven-segmented to nine-segmented; beak short conical, somewhat obscurely two-segmented; no suggestion of marsupium or band of disk pores on ventral face of abdomen---Monophlebulini

bb. Antennae normally 10-segmented (perhaps sometimes with eight segments); beak short conical, one-segmented, and with a definite ventral abdominal pore band surrounding marsupial opening, or beak long conical, distinctly three-segmented, but no marsupium developed. Monophlebini (part only)

aa. Abdominal spiracles without a circle or band of disk pores in atrium just within opening.

c. Derm bearing spines, these varying much in shape; abdominal spiracles probably always in seven pairs, often almost completely obscured.

d. Anal tube with a single to multiple row or band of polygonal wax pores at inner end; antennae normally 10-segmented to 11-segmented---Monophlebini (part only)

dd. Anal tube with a chitinized ring at inner end, but without polygonal or other pores at this point; antennae normally nine-segmented. Llaveiini (part only)

cc. Derm without spines; abdominal spiracles in seven pairs or in as few as two pairs.

e. With a band or definite cluster of disk pores at opening of each thoracic spiracle; abdominal spiracles in seven pairs; antennae 11-segmented; with 3 or with about 30 ventral cicatrices ---- LLAVEIINI (part only)

ee. Without a band or definite cluster of disk pores at opening of each thoracic spiracle; abdominal spiracles, antennae, and cicatrices varying, but never in the above combination.

f. With seven pairs of abdominal spiracles; hairs numerous to very abundant.

g. Hairs numerous, stout, but not crowded, antennae normally 11-segmented; with a single median ventral cicatrix (genus Monophleboides). MONOPHLEBINI (part only)

gg. Hairs very abundant, crowded; antennae normally eight-segmented to nine-segmented; with three large ventral cicatrices, these often very obscure. DROSICHINI

ff. With not more than four pairs of abdominal spiracles; hairs numerous in one genus only, in others very few and perhaps confined to ventral surface; with one to seven ventral cicatrices (possibly wanting in a single species) ---- ICERYINI

LARVA

a. Antennae normally five-segmented.

b. With no spines on body, but with many hairs ---- DROSICHINI

bb. With spines on body, these mostly numerous and conspicuous.

c. Large marginal tubular pores, when present, trilocular; no median ventral cicatrix (uncertain in one genus) ---- MONOPHLEBULINI

cc. Large marginal tubular pores, when present, bilocular; with a median ventral cicatrix, with or without additional lateral cicatrices ---- MONOPHLEBINI

aa. Antennae normally six-segmented.

d. Derm bearing rows of spines dorsally; with seven pairs of abdominal spiracles ---- LLAVEIINI

dd. Derm without rows of spines dorsally; with four or fewer pairs of abdominal spiracles ---- ICERYINI

ADULT MALE

a. Antennal segments beyond second each binodose and bearing two whorls of long setae.

b. Apex of abdomen with more than the single apical pair of fleshy tassels developed; with seven pairs of abdominal spiracles, but the anterior pairs obscure and difficult to locate ---- MONOPHLEBULINI

bb. Apex of abdomen with only the single apical pair of fleshy tassels developed; with not more than four pairs of abdominal spiracles. ICERYINI

aa. Antennal segments beyond second each either trinodose and bearing three whorls of long setae, or anodose and with the setae not grouped in any definite whorls.

c. Apex of abdomen with only the single apical pair of fleshy tassels developed, these short to very long ---- MONOPHLEBINI

cc. Apex of abdomen with at least two, and possibly as many as five or six pairs of fleshy tassels developed, these of various lengths.

d. Basal diagonal vein elongate, somewhat curved at end, this approaching the wing margin closely; costal margin of wing blackish and apical antennal segment about equal to or somewhat longer than preapical, or costal margin bright red and apical antennal segment much longer than preapical (twice). DROSICHINI

dd. Basal diagonal vein short, at its longest fading out without approaching wing margin very closely, not curved toward end; costal margin of wing bright red but apical antennal segment approximately equal to the preapical in length. LLAVEIINI

TRIBE MONOPHLEBINI COCKERELL

This tribe was established by Cockerell (*17, p. 274*) chiefly on the basis of supposedly characteristic male structure, and originally definitely included only the genus Monophlebus. Although not used here strictly as originally defined, this tribal name appears properly assignable to the group of genera discussed below.

Tribal Characteristics

Adult female.—Body shape elongate elliptical, elliptical, broadly elliptical, to ovoid, broader behind; antennae normally 10-segmented to 11-segmented, but variable, in published records ranging from 8-segmented to 12-segmented, usually tapering, with the apical most elongate, the sensory setae sharply differentiated or not; legs usually stout, the setae on the under side of the parts often stout, spinelike, claw digitules slender, short to approximately attaining apex of claw; beak very stout conical, one-segmented, to elongate conical, distinctly three-segmented, apical sensory setae acute to bluntly rounded at tips; thoracic spiracles large, with bar, with or without a definite pore cluster at opening; abdominal spiracles much smaller, simple or with a conspicuous pore collar within atrium, probably always in seven pairs, placed distinctly dorsally, the number of pairs actually present in doubt with a number of the included genera and species; derm pores often very conspicuously developed, heavily chitinized and varying much in size, sometimes nearly uniform and lightly chitinized, the types possibly present including large bilocular tubular, in small clusters along body margin when present, quadrilocular disk, often varying greatly in size, chitinization, and depth, and multilocular disk with various numbers of outer loculi and varying arrangement of the central area, a particular sort of these apparently always associated with genital and anal openings; derm dorsally usually bearing numbers of stout cylindrical spines having rounded tips, these often densely crowded, at least in particular areas, and variously modified, swollen at base and apex, pointed at apex, and so on, ventral derm sometimes with these stout spines along marginal area, or with stout, uniformly tapering, conical spines, the midventral area usually with slender hairs and setae only, the spines rarely continued over this area; with setae scattered over body, not grouped in marginal clusters, sometimes in a definite cluster around anal opening, varying much in size, bases flat to high conical; anal tube usually short and wide, and usually, but apparently not always, with a single or double polygonal wax pore band at inner end; ventral cicatrices varying greatly, from one large oval behind genital opening to three elongate, to perhaps five to seven approximately circular in a transverse curved row, to a considerable number (around 30 or more) in a set of clusters on the under side of the abdomen, to very numerous, in longitudinal bands along both sides of the abdomen, thorax, and head.

Preadult female.—Where definitely known, in general resembling the adult female; with fewer antennal segments, and quantitative reduction in other directions; in some cases, as in Pseudaspidoproctus and Monophleboides, with some structures, as the cylindrical spines, better developed than in the adult.

Larva.—Body elliptical or ovoid, broader anteriorly, derm membranous; antennae five-segmented, stout or slender, the setae on the segments not particularly elongate; legs, in general, relatively large, but not stout, the claw usually slender, somewhat curved, the digitules usually approximating the apex of the claw; beak one-segmented to indistinctly two-segmented or even very obscurely three-segmented, the apical sensory setae acute to bluntly rounded at tips; thoracic spiracles large, with bar, and frequently with a single disk pore at mouth; abdominal spiracles much smaller, usually minute, the openings sometimes with a disk pore adjacent to each, so far as definitely determined in seven pairs, but this uncertain with many species; derm pore types including large marginal tubular bilocular pores, often lacking, quadrilocular disk pores, and multilocular disk pores with varying numbers of loculi and varying arrangement of the centers; dorsal derm with stout spines, in five longitudinal rows, median, marginal, and intermediate, the spines in each row sometimes in clusters, with each cluster outlined by a row of disk pores; derm bearing hairs, apparently on the ventral surface only, and setae, these on both surfaces, those in the posterior middorsal abdominal area sometimes strongly enlarged, the marginal setae large, approximating the apical pair in length, or small and

short, leaving only the apical pair conspicuous, but even these not greatly elongate; anal tube moderately long to rather elongate, with a band of wax pores at inner end, a circle of multilocular disk pores near this end, a ring of special setae, usually short, stout, with flattened, fimbriate tips, around the opening, and outside this a circle of scattered multilocular disk pores; ventral cicatrices one to seven.

Adult male.—Of the usual elongate shape, apex of head more or less distinctly triangular in outline, bearing setae; antennal segments beyond third in two distinct types, one, similar to Drosichini, with each trinodose and with three whorls of setae, the other without nodes, usually cylindrical, and with the setae scattered, not arranged in whorls; wings with the usual subfamily characteristics, the diagonal vein, in all species definitely known from specimens, relatively short, not extending much beyond half the distance from the forking of the veins to the margin along a line representing a continuation of the vein to the margin; halteres of the usual form, flattened, with few to several long, curved, apical setae; legs moderately stout, as in other groups, the anterior femora with a few bifurcate setae; abdomen membranous, the dorsal surface sometimes with darker markings as in Drosicha, with only the two apical fleshy tassels developed, these short to long and bearing setae; abdominal spiracles developed, probably with seven pairs, but sometimes difficult to demonstrate, the posterior pair or pairs sometimes larger and better developed than the anterior ones; derm with the one quadrilocular type of disk pore only, these sometimes with fewer or more loculi; penis sheath, in general, stout, tapering only slightly and more or less uniformly, the apex broadly rounded or sometimes indented medially to form a more or less distinctly bilobate tip.

As will be indicated in some detail later, the genera included here appear, on the basis of a study of the available material, to form two natural groups which may eventually prove sufficiently distinct to justify the establishment of separate tribes for each. While certain differences between the two groups appear to be quite clear-cut and precise, some other characters—for example, the anal tube complex, the five-segmented antennae and the dorsal spine bands in the larva, and the presence of only the apical pair of fleshy tassels in the adult male—appear to be constant throughout all the included genera, and in combination are definitely considered as evidence of relationship. The two groups include the following genera: Group 1, Monophleboides, Monophlebidus, Nietnera, Palaeococcus (?), Perissopneumon, Pseudaspidoproctus; Group 2, Walkeriana, Monophlebus, Labioproctus, Hemaspidoproctus, Aspidoproctus.

The known distribution of the genera and species definitely included here comprises all of the Ethiopian region except Madagascar, the Indian (including Ceylon) and Indo-Malayan subregions of the Oriental region and the Mediterranean subregion of the Palaearctic region. One genus and species, *Palaeococcus fuscipennis* Burmeister, from the European subregion, is not considered in this connection, as specimens have not been available for examination, although it has recently been redescribed by Vayssière (*170, p. 267*). From his discussion it should apparently be placed in this tribe.

Biological information on the members of the tribe is very scant. One species is definitely known to have an annual cycle, with growth during the summer. Green suggests that the species of Walkeriana may grow for several years before reaching maturity.

An attempt is made to separate these genera, so far as the various stages are known, in the keys that follow. Since there are many gaps in the available information regarding various species, these keys will doubtless require critical revision to become satisfactory.

KEYS TO GENERA OF MONOPHLEBINI[20]

ADULT FEMALE

a. Abdominal spiracles relatively large and conspicuous, each with a prominent band of disk pores within the atrium.

b. Ventral cicatrices very numerous (several hundred), small, circular, varying in size, in two broad longitudinal bands, one on each side of abdomen, thorax, and head; presumably secreting a loose mass of flocculent wax threads at oviposition; no suggestion of marsupium or other definite egg receptacle ..... Monophlebidus

bb. Ventral cicatrices less numerous (about 20 to 150), grouped in clusters, these arranged in a semicircle over the ventral abdominal surface; with a definite marsupial opening pore band, and marsupium ..... Perissopneumon

aa. Abdominal spiracles without a band of disk pores just within the atrium of each, often inconspicuous and apparently wanting, actual number present frequently difficult or impossible to determine.

c. Ventral cicatrices very numerous, in a broad band on head, thorax, and abdomen on each side of ventral surface; midventral area with a small, approximately circular marsupial opening, normally covered by a layer of white felted secretion and bordered by a heavy band of disk pores, this opening leading to a greatly enlarged internal marsupium; size large to very large; often ornamented dorsally with prominent spikes or ridges; distribution Central and South Africa ..... Aspidoproctus

cc. Ventral cicatrices not very numerous, not forming broad longitudinal bands; marsupial opening, if marsupium is present, either slitlike, or U-shaped, or V-shaped, and without pores in the rim.

d. Ventral cicatrices apparently wanting, actually minute, very inconspicuous, each circular, arranged in a few vague segmental rows or clusters on each side of ventral surface near posterior apex, total number present intermediate (perhaps about 30); no marsupium or ovisac pore band; no large marginal bilocular tubular pores; Ceylon ..... Nietnera

dd. Ventral cicatrices not more than about seven, arranged transversely across abdomen behind genital opening, in any event relatively and often actually large and conspicuous.

e. Ventral surface of abdomen with a band of pores, comparable to the ovisac band of Icerya, this forming a pad of dense secretion over the enclosed area, and with the ventral abdominal wall tending to invaginate forming a half-marsupium; derm pores and spines numerous; ventral cicatrices five to seven ..... Hemaspidoproctus

ee. Ventral abdominal surface either unmodified, or with a definite marsupium having a U-shaped or V-shaped opening, not covered by a secretionary pad; ventral cicatrices one to three.

f. Margins of body with clusters, apparently segmental, of from one to several medium to large tubular, bilocular pores; derm bearing numerous cylindrical or pointed spines, often densely crowded in certain areas at least, and numerous disk pores, with the quadrilocular type conspicuous, but varying much in size and extent of chitinization.

g. With an internal marsupium, the entrance midventral, slitlike or V-shaped ..... Labioproctus

gg. Without an internal marsupium or other special modification connected with reproduction; eggs (or larvae) presumably deposited directly beneath body ..... [21] Walkeriana

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[20] Only genera for which specimens are available have been included here. This eliminates Monophlebus and Palaeococcus.

Additional genera are omitted in the separate keys where not represented by specimens; e. g., the larval key omits Perissopneumon and Monophlebidus.

[21] *Walkeriana senex* Green, with a definitely developed ovisac, does not fit into this key; it may be more closely allied to Hemaspidoproctus than to Walkeriana, or may represent a distinct and undescribed genus.

ff. Derm without tubular bilocular pores at margin or elsewhere; derm spines, even where rather numerous, not densely crowded in any area; quadrilocular pores, if present at all, small and very inconspicuous, none of the pores very heavily chitinized.

h. Derm with cylindrical spines present, often numerous; with an abdominal marsupium, the opening approximately U-shaped, with the curve posterior; with three elongate to very elongate ventral cicatrices placed close together on the ventral surface behind the marsupial opening ..... Pseudaspidoproctus

hh. Derm without cylindrical spines (present and numerous in preadult stage); no traces of marsupium, forming a loose mass of secretion at oviposition time; with a single ventral cicatrix (perhaps not a generic characteristic) ..... Monophleboides

LARVA [22]

a. Body without a row of large bilocular tubular pores, secreting glassy threads, along margin.

b. With more than one pair of conspicuous apical setae, although with one pair somewhat longer; with conspicuous lateral marginal setae in addition; antennae slender, with third and apical segments elongate. Pseudaspidoproctus

bb. With only a single apical pair of elongate setae; no elongate lateral setae.

c. Antennae relatively short and stout, the third segment little, if any, longer than the second; with a single, rather large, median, ventral cicatrix; body spines few, stout cylindrical, curved. Monophleboides

cc. Antennae elongate, rather slender, third and apical segments much elongated; no median ventral cicatrix, but several (six) small, in a transverse curved row; body spines numerous, stout lanceolate with attenuated tips ..... Nietnera

aa. Body with a row of conspicuous, large, bilocular tubular pores, secreting glassy threads, along margin; antennae short and stout, the third segment in particular not especially elongate.

d. Marginal setae relatively elongate, some, at least, often approaching or attaining the length of the apical pair; a single median ventral cicatrix.

e. Dorsal spines grouped in clusters partially outlined by transverse rows of quadrilocular disk pores ..... Walkeriana

ee. Dorsal spines in five longitudinal rows, but not split up into clusters by transverse rows of quadrilocular disk pores.

f. Collar of disk pores within anal tube made up of only about four to six well separated pores. Hemaspidoproctus

ff. Collar of disk pores within anal tube continuous, and sometimes double, including 10 to 12 or even more pores (perhaps not a generic character). Labioproctus

dd. Marginal setae relatively very short, hardly exceeding marginal spines in length, the apical setae, in consequence, although short, relatively conspicuous; more than one ventral cicatrix. Aspidoproctus

ADULT MALE [23]

a. Antennal segments beyond second distinctly trinodose and each with three conspicuous and sharply segregated whorls of setae, closely resembling Drosicha; Central and South Africa ..... Aspidoproctus

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[22] In addition to the genera omitted from all keys, Monophlebidus and Perissopneumon are omitted from this because of lack of specimens.

[23] Besides the genera wholly omitted from the keys, the genera Hemaspidoproctus, Walkeriana, and Perissopneumon are omitted from this key as the adult male is not definitely known for any of them.

aa. Antennal segments beyond second, while often somewhat trinodose, with the whorls at most indefinitely formed, more often anodose and without a clear suggestion of whorls of setae.
b. Apical abdomnial fleshy tassels very short, almost knoblike; African. Monophleboides
bb. Apical abdominal fleshy tassels much longer, tapering, approaching or approximating the abdomen in length.
c. Apical fleshy tassels about two-thirds as long as abdomen; preapical antennal segments fairly evidently trinodose, with the setae forming very loosely clustered whorls (not certainly generic characters); Ceylon ---------- Labioproctus
cc. Apical fleshy tassels at least closely approximating the abdomen in length; preapical antennal segments at most somewhat irregularly nodulose, but with no definite suggestion of either nodes or whorls of setae (not certainly generic characters).
d. Penis sheath elongate conical, tapering uniformly to the bluntly rounded apex (from description only) (perhaps not a generic character); African ---------- Pseudaspidoproctus
dd. Penis sheath elongate and slender, but constricted slightly toward apex, this portion more nearly cylindrical than basal part; tip rather acutely rounded (perhaps not a generic character); Indian ---------- Monophlebidus

GROUP 1

This group of genera, on the basis of the material available for study, is segregated from the following group by the absence in both the first-stage larva, where they would be conspicuous, and in the adult female, where they are frequently obscured, of the large bilocular tubular pores responsible for the secretion of glassy threads in both stages. The genus Perissopneumon Newstead, as redescribed below, resembles Walkeriana and its relatives quite closely in the pronounced development of the spines; and the lack, for study purposes, of larval stages of the included species is the weakest point in the grouping here indicated, since if they proved to have the large marginal tubular pores this would break down the grouping of the genera that is given here.

Genus Monophleboides Morrison

(Pl. 3, F, and figs. 57, 58, and 59)

This genus has just been established by the writer (*136, p. 104*) with a North African species as genotype. The discussion in connection with the genus Palaeococcus, immediately following, should be examined for additional information as to its probable status.

GENERIC CHARACTERISTICS

Habit.—Living exposed on the host plant; at maturity producing a loose mass of eggs more or less covered with cottony secretion.

Adult female.—Body nearly uniformly elliptical, convex, this more pronounced posteriorly, character of secretion not certain; body, as mounted, elongate ovate, broader behind; antennae normally 11-segmented, the basal broad, the remainder tapering, the sensory setae not clearly differentiated; legs stout but small, with some of the setae on the undersides of femur, tibia, and tarsus stout spinelike, claw not particularly stout, somewhat curved, digitules stout, tapering strongly, much shorter than the claw itself; beak conical, of medium length, obscurely two-segmented, the apical sensory setae few and with acute tips; thoracic spiracles with bar, without a definite pore cluster at apex; abdominal spiracles in seven pairs, inconspicuous, the opening proper only

lightly chitinized; derm pores of one sort only, multilocular disk, not heavily chitinized, circular, with center varying from circular to bilocular, and number and size of loculi varying; derm without spines, as here recognized, with numerous, but not crowded, large, rather stout hairs both dorsally and ventrally; with scattered setae, these varying much in size, those along body margin much larger, all with short and usually rather flat conical bases; anal tube short, faintly chitinized, with a thickened ring, but no wax pores at inner end, opening into a cluster of hairs plus a few setae; with a single median ventral cicatrix.

Preadult female.—In general resembling the adult; with fewer antennal segments, size somewhat smaller and, here differing most conspicuously, derm with numerous but not crowded, elongate cylindrical, curved spines, the mid-ventral area with small setae and minute hairs.

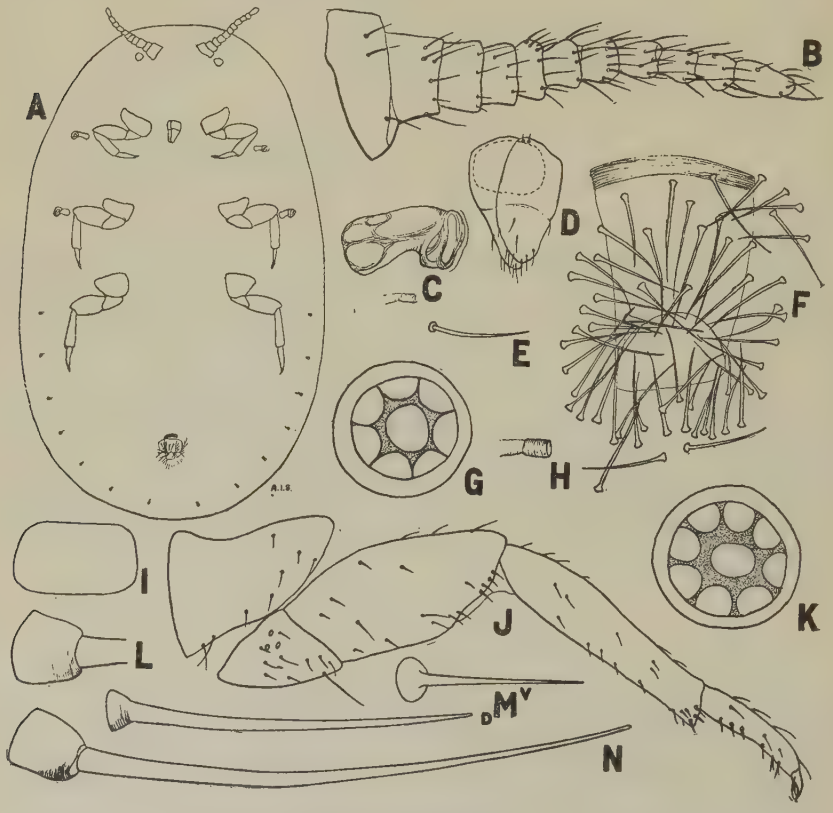

FIG. 57.—*Monophleboides gymnocarpi*, adult female: A, outline, optical section, × 7.5; B, antenna, × 60; C, thoracic and abdominal spiracles, × 60; D, beak, × 60; E, beak sensory seta, × 230; F, anal area, × 115; G, dorsal disk pore, × 1,500; H, abdominal spiracle, × 120; I, ventral cicatrix, × 30; J, leg, × 50; K, ventral disk pore, × 1,500; L, base of largest type marginal seta, × 650; M, ventral (v) and dorsal (D) hairs, × 650; N, dorsal seta, × 650

Larva.—Body nearly uniformly elliptical; derm membranous; antennae five-segmented, rather short and stout, the second and third approximating each other in length, apical segment with about four somewhat stouter sensory setae at apex; legs not unusual, bearing slender setae, trochanters with two sensory pores on each face, claw very slightly curved, with subapical denticle, claw digitules acute, slightly exceeding half the claw in length, not approaching claw apex; beak medium conical, indistinctly two-segmented or perhaps even indefinitely three-segmented, apical sensory setae acute; thoracic spiracles large, with broad bar and single disk pore at opening; abdominal spiracles small, but evident, in seven pairs, each with invaginated inner end; derm pores of a single type, mostly circular to somewhat quadrate, with circular to

oval centers and normally four loculi, spiracular and anal tube disk pores circular with about eight loculi; derm bearing stout, nearly cylindrical spines, mostly in pairs or clusters, along body margin, bearing some small slender hairs ventrally and stout, blunt-tipped setae dorsally and slender acute setae ventrally in longitudinal rows; anal tube of medium length, with a double collar of polygonal wax pores at inner end, a circle of multilocular disk pores just before this, and a ring of more or less flattened short setae on derm around opening; with a single median ventral cicatrix of medium size.

Adult male.—Of the usual elongate form, small, apex of head triangular in outline and bearing a few stout setae; antennae 10-segmented, distinctly shorter than the body, the segments beyond the third not nodose, and the setae on them not in distinct whorls,[24] these setae relatively stout, tapering somewhat, with tiny flattened tips, apical antennal segment not longer than preapical; legs fairly stout, the anterior femora with about six bifurcate setae, the claws slender, all observed nearly straight (possibly distorted), claw digitules spine-like, hardly extending to middle of claw; wings not unusual, the diagonal vein quite short, not extending half way to the wing margin, halter lobe of wing relatively long protuberant; halteres small, flattened, usually with four

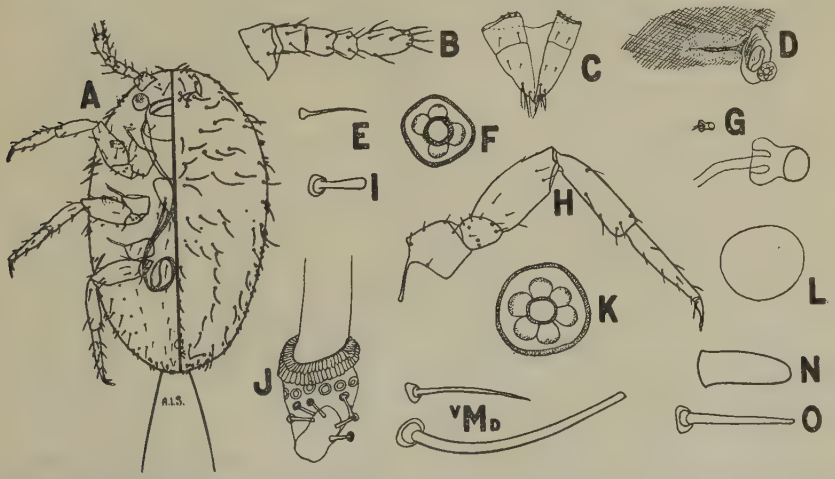

FIG. 58.—*Monophleboides gymnocarpi*, larva: A, outline, dorsal and ventral, × 60; B, antenna, × 120; C, beak, × 120; D, thoracic spiracle, × 460; E, ventral derm hair, × 650; F, derm pore, × 1,500; G, abdominal spiracle, above × 460, below × 1,500; H, leg, × 115; I, seta close to anal opening, × 650; J, anal tube, × 330; K, disk pore from anal tube, × 1,500; L, ventral cicatrix, × 330; M, body setae, dorsal (D) and ventral (V), × 650; N, derm spine, × 650; O, marginal seta, × 650

stout, curved, knobbed setae; abdomen, as mounted, with curving sides, broadest about the middle, bearing a few stout setae in transverse rows dorsally and ventrally, and clusters of somewhat larger setae at margins of segments, apex with a pair of short, stout lobes bearing still longer stout setae; penis sheath small and stout, tapering somewhat, but broad and slightly but distinctly indented at the apex, the base transversely truncate; abdominal spiracles probably in seven pairs (only six distinctly located), the posterior large, relatively heavily chitinized and conspicuous, the remainder smaller, obscure, or at least often difficult to make out definitely; with the usual quadrilocular disk type of pore; body setae, as stated, stout, mostly with blunted apices.

The genotype and, at present, only positively included species is *Monophlebus gymnocarpi* Hall (*86, p. 1; 87, p. 113*) from Egypt. It seems possible, from an examination of their respective descriptions, that the species *M. africanus* Newstead (*149, p. 15*), from

[24] Hall (*86, pl. II, fig. 1*) figures the third antennal segment of the male, which he described, as trinodose and with three whorls of setae.

Southwest Africa, *M. hirtus* Brain (*3, p. 165*), from Cape Province, *M. sjostedti* Newstead (*145, p. 2*), from Tanganyika Territory, and *M. suaedae* Vayssière (*169, p. 29*), from Tunis, all African species, may properly belong here, but such assignment can not be made positive in the absence of specimens of these species. The comment

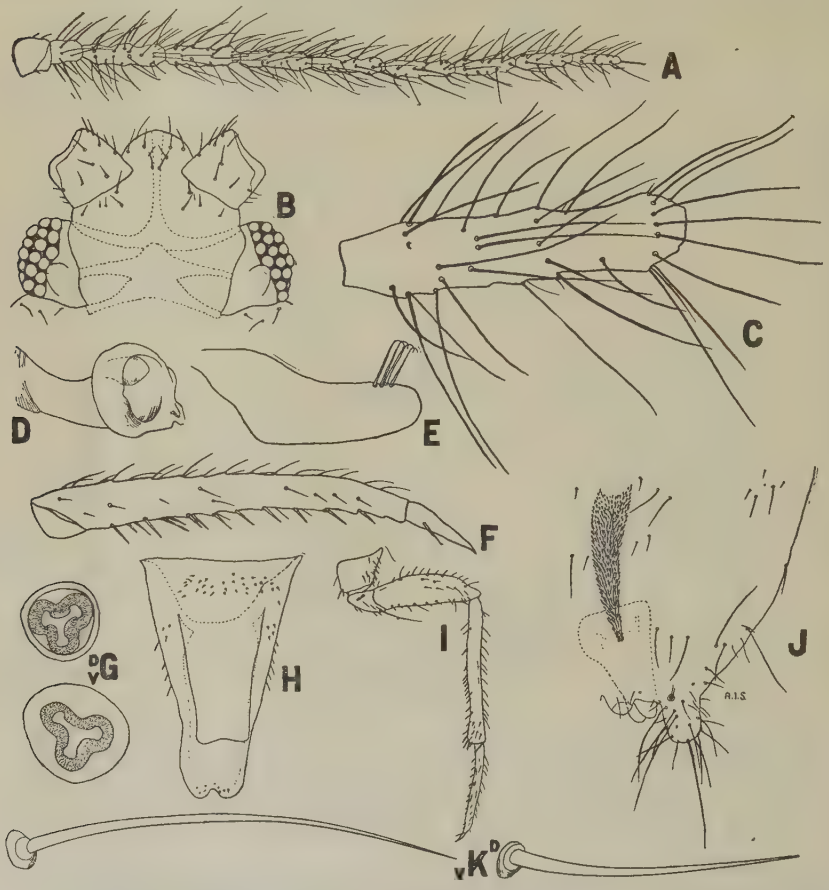

FIG. 59.—*Monophleboides gymnocarpi*, adult male: A, antenna, × 30; B, head, dorsal, × 60; C, third antennal segment, × 120; D, abdominal spiracle, × 530; E, halter, × 120; F, tarsus and claw, × 120; G, dorsal (D) and ventral (V) abdominal disk pores, × 1,500; H, penis sheath, ventral, × 120; I, middle leg, × 30; J, apex of abdomen, dorsal and optical section, × 60; K, ventral (V) and dorsal (D) setae, × 650

on this genus in connection with the discussion of Palaeococcus should also be examined.

The genotype has been found in Egypt.

According to Hall, fertilization of the female of the genotype occurs in early April, oviposition from the middle to the end of May, and first appearance of the larvae immediately thereafter.

GENUS PALAEOCOCCUS COCKERELL

The generic name Palaeococcus was proposed by Cockerell (*8, p. 36*) in 1894 to replace the preoccupied generic name Leachia which

had been erected by Signoret (*158, p. 359*) in 1875 for two species, *Monophlebus fuscipennis* Burmeister and *M. brasiliensis* Walker. No type was set by Signoret at the time of the original description of the genus, or by Cockerell when he replaced Leachia with Palaeococcus. The first definite type citation appears to have been made by Cockerell (*23, p. 233*) in 1902, when *fuscipennis* was designated positively as genotype. Lindinger's references to the genus (*113, p. 53, 257, 282*) are not certainly, from the context, based on an examination of specimens, but the recent extended paper by Vayssière (*170, p. 256, 267*) gives a discussion of the value of Palaeococcus as a genus and of the characteristics of its genotype. In view of the ample evidence from other sources that there are a number of valid genera in this tribe now known from the Oriental region, and that none of their included species possess characteristics closely resembling those of *Palaeococcus fuscipennis*, it does not seem possible to accept Vayssière's apparent conclusion that Palaeococcus is inseparable from Monophlebus. It seems certain that it is actually a valid genus zoologically, and one not very intimately related to the genus Monophlebus as this is represented by its genotype, *M. atripennis* Burmeister.

Because of some discrepancies between the original description of *Palaeococcus fuscipennis* and that just offered by Vayssière, because of the geographically well separated sources of the specimens on which these descriptions were based (Berlin, Germany, for the original, and southern France and central Spain for that of Vayssière), and because of a definite reluctance to accept as final some of the stated characteristics given in Vayssière's excellent description,[25] it has seemed best to refrain from any attempt to incorporate the genus Palaeococcus into this work on the basis of literature only.

From a review of these available descriptions, it appears practically certain that Palaeococcus belongs properly in the tribe Monophlebini and that it is most closely related to the genus Monophleboides, discussed in the pages just preceding. Indeed, the writer confidently anticipates that fuller information on these genera and their included species will show clearly that the two genera are identical zoologically and that they may in consequence be synonymized. However, no such action can be taken on the basis of existing knowledge.

Genus Nietnera Green

(Figs. 60 and 61)

This genus was described by Green (*65, p. 455*) in 1922, with the single included species *N. pundaluoya*. No additional species have been recognized as belonging to the genus. The characterization offered below is based on specimens kindly presented for study purposes by Green.

GENERIC CHARACTERISTICS

Habit.—Living exposed on the leaves and stems of the host.

Adult female.—Body ovoid, broader behind, bearing a thin film and long tufts of secretion; body as mounted nearly stout ovoid, only slightly broader

[25] For example, the adult female ought, from its other characteristics, to have a single, median, approximately circular ventral cicatrix.

behind, posterior apex with a distinct median notch; derm membranous to more or less heavily chitinized at maturity; antennae normally 11-segmented, elongate, tapering somewhat, stouter sensory setae wanting on the segments examined; legs stout, setae stiff but not spinelike, condition of claw and digitules uncertain; beak stout conical, indefinitely two-segmented, with some apical sensory setae; thoracic spiracles well developed, with broad bar and conspicuous oblong cluster of disk pores at mouth; abdominal spiracles much smaller but evident, in seven pairs, simple, somewhat bell-shaped, the posterior pair very close to anal opening; derm pores of one type only, large, circular to somewhat oval with around 10 loculi and circular, to oval, to linear, to sometimes triangular centers; derm dorsally crowded with short stout spines; ventrally with numerous relatively long stout hairs; some setae present, these resembling the hairs in appear-

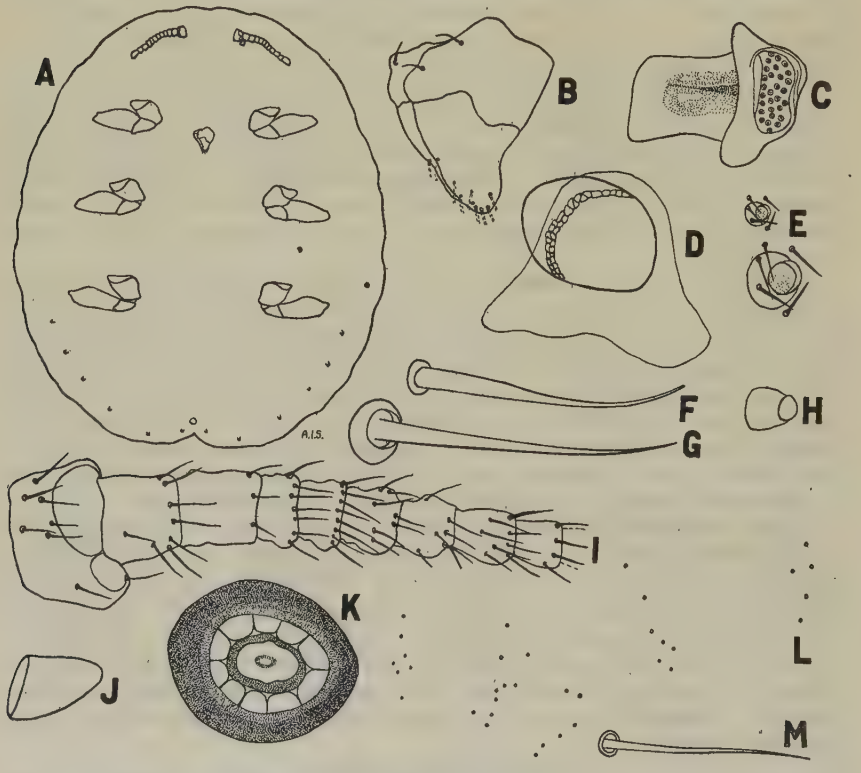

FIG. 60.—*Nietnera pundaluoya*, adult female: A, outline, optical section, × 11; B, beak, × 60; C, thoracic spiracle, × 60; D, anal tube, × 650; E, abdominal spiracle, above × 60, below × 120; F, ventral seta, × 650; G, body seta, × 650; H, apical abdominal spiracle, × 120; I, antenna (incomplete), × 60; J, derm spine, × 650; K, derm disk pore, × 1,500; L, clusters of ventral cicatrices on right half of ventral surface of abdomen behind genital opening, × 30; M, ventral submarginal seta, × 650

ance; anal opening almost apical, anal tube short, with a double row of polygonal wax pores at inner end; ventral cicatrices apparently lacking but, if correctly identified, actually present but very inconspicuous, circular, each little larger than a disk pore, in a few very scattered segmental clusters near posterior apex of body.

Larva.—Relatively large, uniformly elliptical as mounted; derm membranous; antennae rather slender, five-segmented, the third and apical segments elongated, the third much longer than the second, apical segment with several somewhat stouter sensory setae; legs medium, trochanters with two sensory pores on each face, tarsal claw moderately curved, with two or three small denticles on inner face of apical half, claw digitules elongate, slender, very slightly knobbed, surpassing apex of claw; beak stout conical, obscurely two-

segmented, with several blunt-tipped apical setae; thoracic spiracles large, with wide bar and three or four disk pores in row at opening of each; abdominal spiracles much smaller, but evident, in seven pairs, not accompanied by disk pores; derm pores of two types, one multilocular disk, circular to oval, with circular to oval center and around 10 loculi, the other smaller, quadrilocular

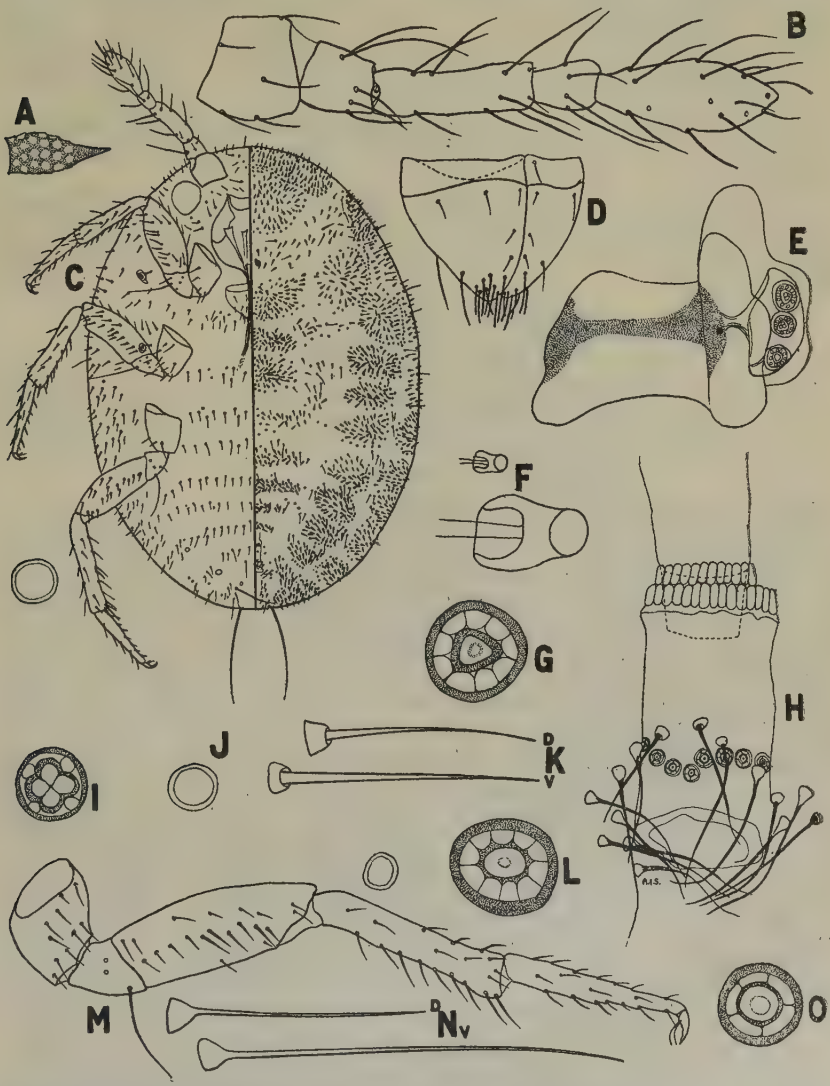

FIG. 61.—*Nietnera pundaluoya*, larva: A, derm spine, × 650; B, antenna, × 120; C, outline, dorsal and ventral, × 30; D, beak, × 115; E, thoracic spiracle, × 460; F, abdominal spiracle, above × 460, below × 1,500; G, midventral derm disk pore, × 1,500; H, anal tube, × 330; I, middorsal derm disk pore, × 1,500; J, ventral cicatrices from left half of ventral surface of abdomen, × 330; K, derm setae, dorsal (D) and ventral (V), × 650; L, ventral derm pore, × 1,500; M, leg, × 165; N, derm hairs, dorsal (D) and ventral (V), × 650; O, disk pore from anal tube, × 1,500

disk, but apparently with four additional small circular loculi, the first present in small numbers on the ventral surface, the second frequent dorsally, particularly in rows partially outlining the clusters of spines; derm with numerous spines dorsally in segmental median, intermediate, and marginal clusters, these in combination also forming five longitudinal bands with many of the individual

clusters outlined by partially encircling rows of quadrilocular disk pores, the individual spines stout lanceolate, showing distinct reticulate or areolate structure; derm with slender hairs both dorsally and ventrally and with slender setae, these much more numerous ventrally; anal tube fairly elongate, with a double band of polygonal wax pores at inner end and a single circle of multilocular disk pores nearer to opening than inner end, anal opening with slender hairs and setae adjacent, but no short stout ones; with a single enlarged pair of apical setae and no enlarged marginal setae; without a median ventral cicatrix, but with six small circular ones arranged in a transverse curved row near the posterior apex of body.

There is little information available regarding the life history of this insect, and no definite suggestions have been made as to the annual or other life cycle.

While this genus pretty certainly belongs with the group of genera to which it is here assigned, there is some difficulty in indicating its closest relatives. Probably they will be found in Monophlebidus and Perissopneumon.

Genus Monophlebidus Morrison

(Pl. 4, A, and figs. 62 and 63)

This genus has just been named by the writer (*136, p. 104*) on the basis of a species, *M. indicus* Morrison, described at the same time.

GENERIC CHARACTERISTICS

Habit.—Uncertain, presumably ovipositing beneath the body at maturity.

Adult female.—Elongate elliptical, dorsally with a coating of secretion, and with transverse bands of denser and lighter secretion, margin with a series of short tufts of secretion; derm tending toward slight chitinization; antennae normally 10-segmented, tapering, the setae stout, fairly numerous, some sensory setae slightly differentiated; legs stout, some of the setae on under sides of femur, tibia, and tarsus quite stout, spinelike, claw stout, somewhat curved, claw digitules slender, delicate, approaching the apex of the claw; beak elongate conical, distinctly three-segmented, the basal segment a narrow ring, apical sensory setae acute at tips; thoracic spiracles large, the posterior larger than anterior, each with bar and a definite cluster of multilocular disk pores at opening; abdominal spiracles in seven pairs, large, conspicuous in spite of the densely crowded spines, urn-shaped, with a wide band of multilocular disk pores within the atrium of each; derm pores not varying greatly in size, of one general type, multilocular disk with fairly heavily chitinized rim, with about 11 loculi and with centers with three, four, or five lobes, these abundant over both surfaces; spines very abundant, most of those on dorsal surface elongate, curved, nearly cylindrical, with somewhat enlarged bases and bluntly rounded apices, some elongate conical, tapering uniformly to acute tips, ventral surface with the elongate conical sort, accompanied by numerous disk pores, here in transverse bands separated by narrow but distinct bare stripes; setae relatively scarce, varying in length and stoutness, mostly with rather long conical bases; hairs few, small and inconspicuous, scattered over both surfaces, more numerous ventrally; anal tube large, elongate, definitely chitinized, with a broad band of wax pores at inner end and a double row of small disk pores near mouth; ventral cicatrices small, very numerous (with several hundred), arranged as in Aspidoproctus, that is, extending along the margin of the ventral surface in a band on each side, this running from the head to behind the genital opening, each band made up of transverse rows of circular cicatrices varying considerably in size.

Intermediate female.—Closely resembling the adult.

Larva.—Not available.

Adult male.—Of the usual elongate shape, size moderate (body proper about 5 mm.), apex of head triangular with tip rounded, bearing numerous long setae; antennae shorter than body proper, the segments beyond the third cylindrical, not nodose, and with the setae not arranged in definite whorls, the apical segment at most only a little longer than the preceding; wings quite dark, tending toward a point at apex, the diagonal vein extending little more than half way

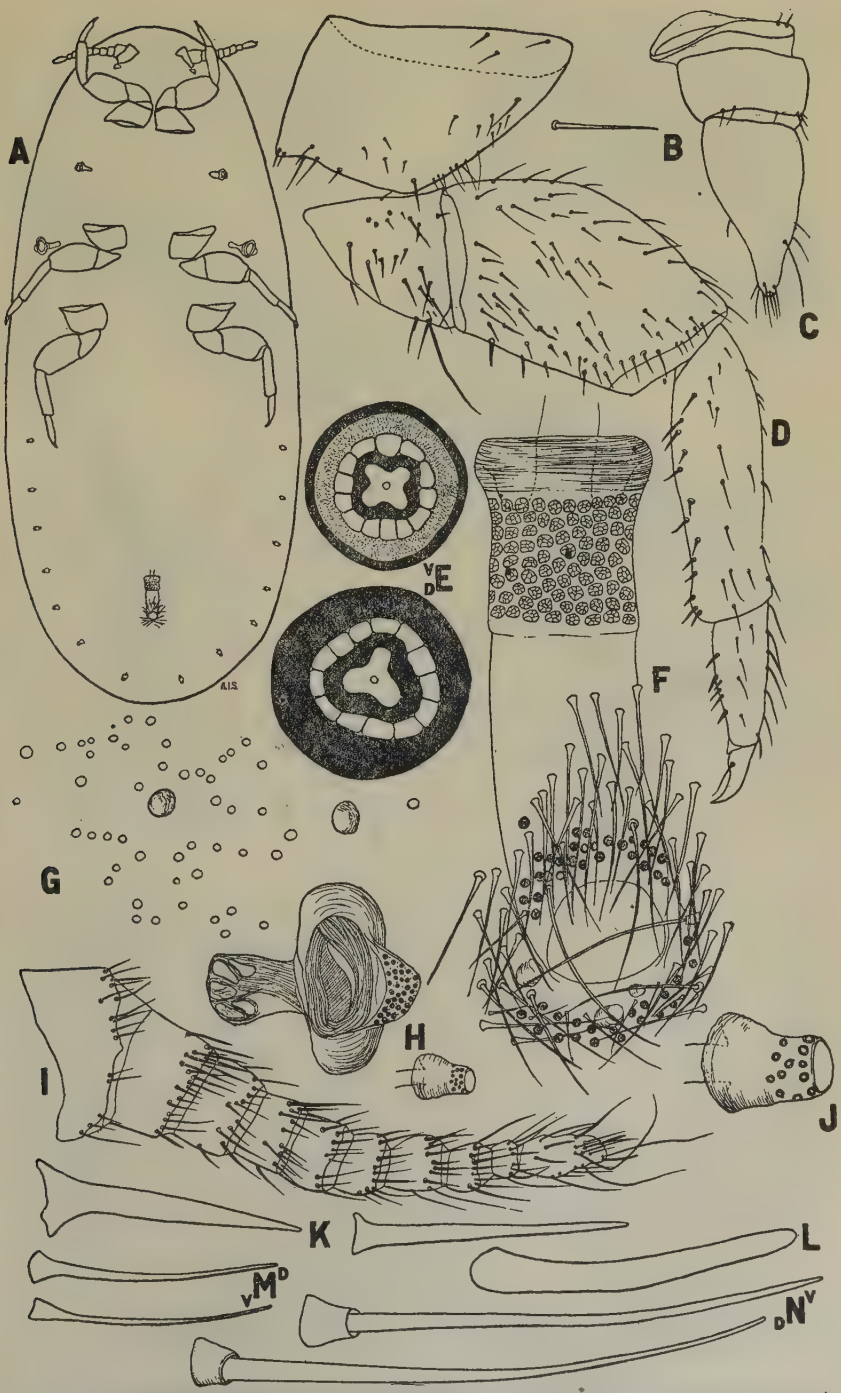

FIG. 62.—*Monophlebidus indicus*, adult female: A, outline, × 7.5; B, beak sensory seta, × 230; C, beak, × 60; D, leg, × 50; E, derm pores, ventral (V) and dorsal (D), × 1,500; F, anal tube, × 120; G, small group of ventral cicatrices, × 60; H, thoracic and abdominal spiracles, × 60; I, antenna × 60; J, abdominal spiracle, × 120; K, ventral spines, × 650; L, dorsal spine, × 650; M, dorsal (D) and ventral (V) hairs, × 650; N, ventral (V) and dorsal (D) setae, × 650

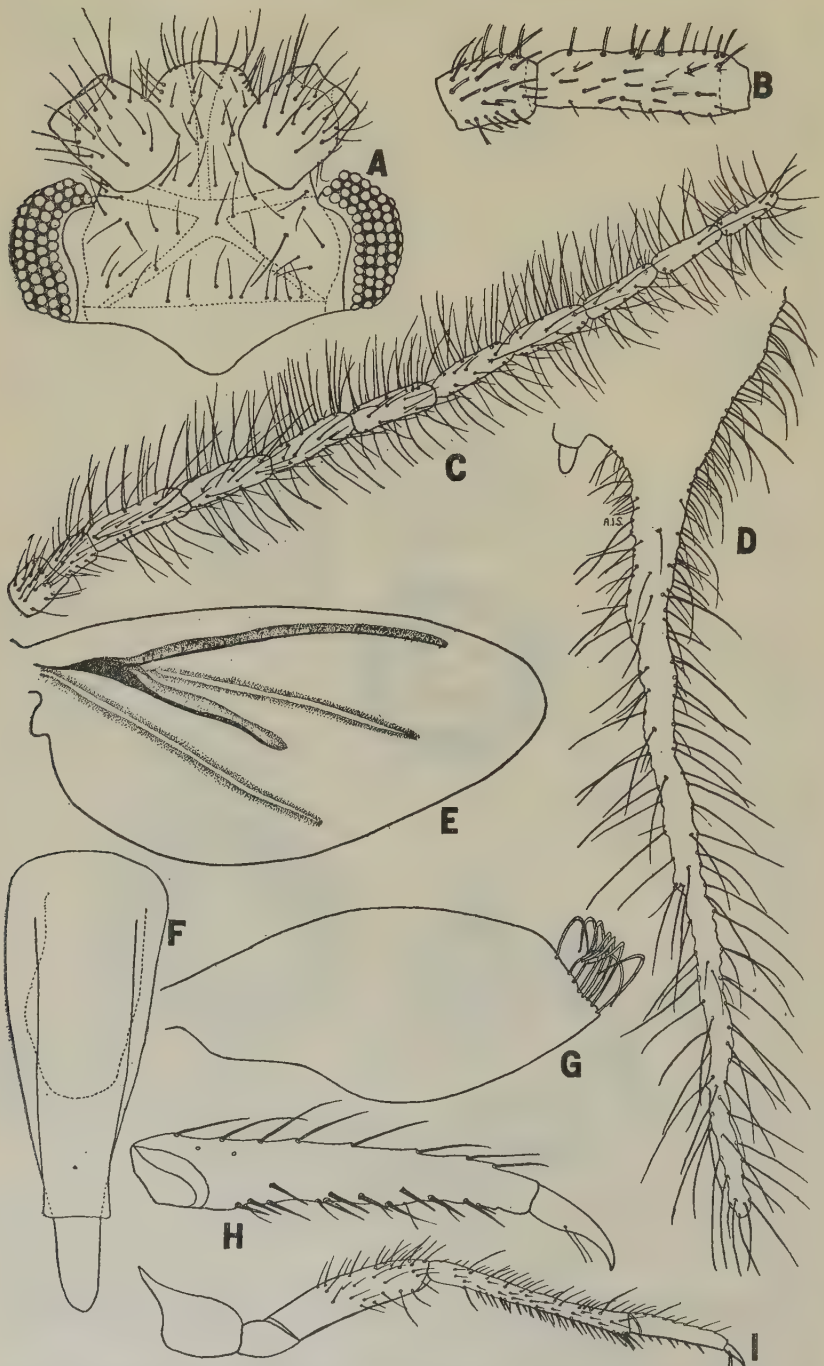

FIG. 63.—*Monophlebidus indicus*, adult male: A, head, dorsal, × 60; B, second and third antennal segments, dorsal, × 60 (setae abbreviated); C, antenna, × 30; D, apex of abdomen, × 50; E, wing, × 17.5; F, penis sheath, ventral, × 80; G, halter, × 120; H, tarsus and claw, × 60; I, entire leg, × 30

to the wing margin; halteres rather large, flattened, with about nine knobbed setae at apex of each; legs rather stout, bearing numerous setae, the anterior femora with only one or two bifurcate setae, claw rather stout, slightly curved, digitules slender, not attaining apex of claw; abdomen with some transverse chitinized markings, the sides nearly parallel, converging somewhat behind, bearing at apex a single pair of fleshy tassels, these slender, tapering somewhat, nearly as long as abdomen; penis sheath elongate and slender as compared with other genera, tapering rather gradually but not uniformly from base to apex; abdominal spiracles not observable, presumably in seven pairs; derm pores of the usual quadrilocular disk type; derm setae rather large and long as compared with other males examined.

No species other than the genotype have been recognized as assignable to this genus. The known distribution is therefore limited to the Indian subregion of the Oriental region. There is no information available regarding the biology of the single included species.

Genus Perissopneumon Newstead

(Pl. 4, B, and figs. 64 and 65)

This genus was described by Newstead (*142*, *p. 250*) in 1900 from specimens obtained from ant nests (probably ant cartons) near Bombay, India. The only included species, which appears never to have been rediscovered, was *ferox* Newstead. The genus was placed as a synonym of Hempel's genus Stigmacoccus by Cockerell (*23*, *p. 233*) in 1902 and was also so considered in the Catalogue of the Coccidae of the World (*46*, *p. 20*) although this was not accepted by the author of the genus (*147*, *p. 157*). One species collected in India seems properly assignable here, and two others, one from the Philippines and one from Java, have been studied in connection with the generic diagnosis offered here. It is not considered probable that the Indian species examined is the genotype because of certain differences between its structure and that given in Newstead's description.

GENERIC CHARACTERISTICS

Habit.—Uncertain in some respects; living exposed on the bark and branches of the host or protected by ants; eggs deposited within a large internal marsupium having a midventral opening.

Adult female.—Of moderate size (about 10 to 12 mm.), with a rather dense but not thick coating of wax over the surface; uniformly broad elliptical, strongly elevated, approaching a semicircular cross section at maturity, usually with lateral longitudinal ridges; derm membranous or tending toward slight chitinization and densely crowded with spines; antennae normally 10-segmented, sometimes with fewer (genotype said to have eight), stout, tapering, basal segments tending to be broader than long, sensory setae not sharply differentiated from others; legs stout, some of setae on under sides of femur, tibia, and tarsus slender, not stout spinelike, claw stout, curved, claw digitules slender, probably approaching the tip of the claw; beak very stout conical, one-segmented, sensory setae, if present, few in number and acute at apices; thoracic spiracles large, with wide bar and with distinct large disk pore cluster at opening; abdominal spiracles in seven pairs, and while much smaller than thoracic, also large, with a distinct broad collar of disk pores within atrium of each; derm pores of two general types, quadrilocular and multilocular disk, the long tubular bilocular type found along margin in some genera wanting, these pores varying markedly in respect to number of loculi, extent of chitinization, size, and detailed modifications of internal arrangements; some, including both quadrilocular and smaller multilocular, forming a definite ventral abdominal band surrounding the marsupial opening; derm spines very numerous and densely crowded dorsally, but not segregated into definite clusters as in Walkeriana; these spines all, in general, large, stout, more or less curved, with somewhat swollen bases and bluntly rounded apices, those present ventrally, including those within the mar-

supial opening band, stout, straight or nearly so, and sharply pointed at apices; hairs small and inconspicuous, slender, most readily observed on the ventral derm within the marsupial opening pore band; relatively small and inconspicuous setae present on both surfaces, these with stout cylindrical or short conical bases; anal tube more or less chitinized, the inner end with a double row of wax pores, the opening surrounded by a cluster of very heavy walled multilocular disk pores and by some of the acute-tipped stout spines occurring elsewhere on the ventral surface only; ventral cicatrices fairly numerous (about 20 to 50), arranged as with Llaveia in a large half oval made up of a series of small clustered or individual cicatrices, with a median posterior one larger.

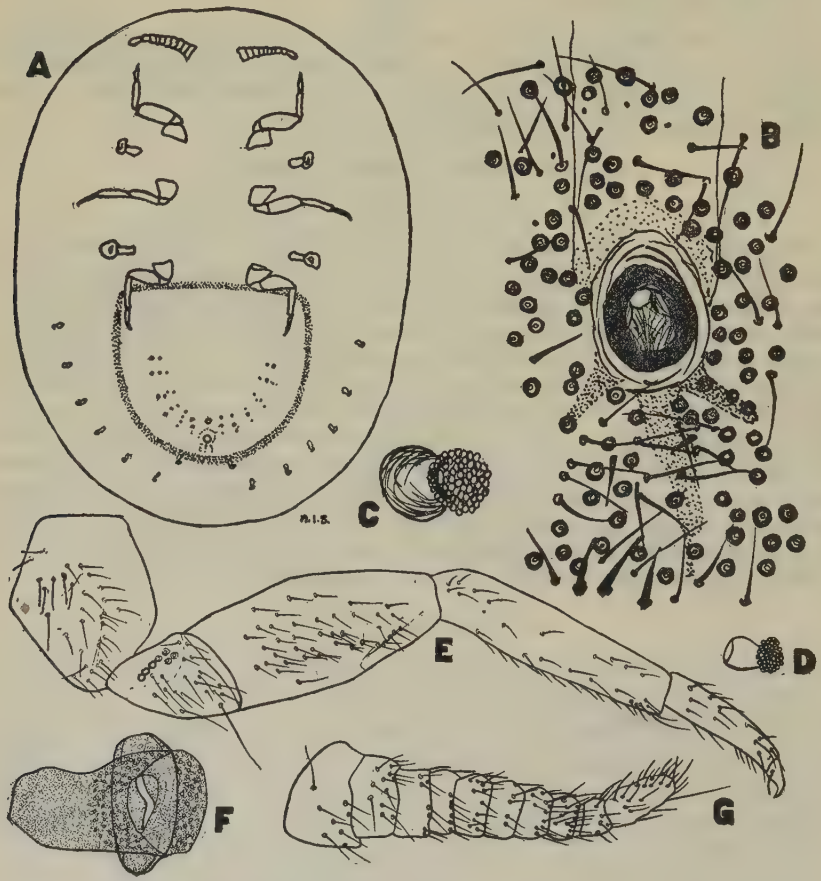

FIG. 64.—*Perissopneumon convexa*, adult female: A, outline, × 7.5; B, anal area, × 165; C, abdominal spiracle, × 120; D, abdominal spiracle, × 57.5; E, leg, × 57.5; F, thoracic spiracle, × 57.5; G, antenna, × 57.5

Intermediate female.—In general resembling the adult female, size smaller, antennae with fewer segments, and with spines, hairs, setae, and pores much fewer, but approximately identical in distribution; ventral cicatrices numerous, but fewer than in adult, and, perhaps most important, abdominal spiracles, while large, without any pore collar within the atrium.

No other stages known.

The distribution of the species included here (India, the Philippine Islands, and Java) covers the three larger of the four Oriental subregions.

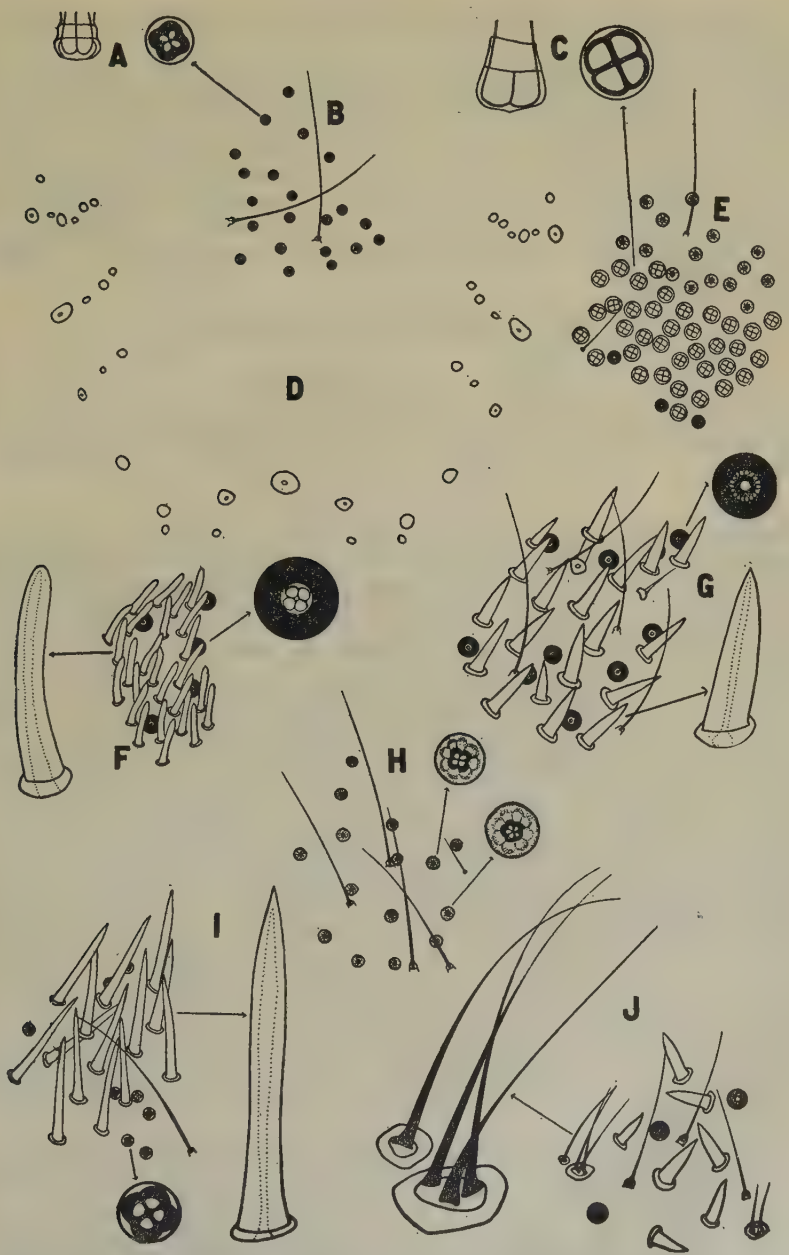

FIG. 65.—*Perissopneumon convexa*, adult female: A, detail of quadrilocular pores placed ventrally posterior to beak, × 640; B, gross view of portion of same region, × 165; C, detail of pores from heavy band present ventrally in abdominal region, × 640; D, ventral cicatrices, showing large number and arrangement, × 30; E, portion of band mentioned under C, × 165; F, dorsal pores and spines, × 165, detail drawings, × 640; G, ventral submarginal spine, pore, and hair group, × 165, details of first two, × 640; H, pores and hairs occurring ventrally near genital opening, × 165, detail of gland, × 640; I, ventral spines, pores, and hairs near pore band mentioned under C, × 165, details of spine and pore, × 640; J, from same region as G, × 165, showing occasional development of more than one hair from a single base, with detail, × 640

Nothing definite seems to have been published regarding the biology of these species.

Of the lots of material studied in connection with work on this genus, only those representing the species described as *Lophococcus convexus* Morrison (*133, p. 153*), from the Philippine Islands, have been definitely identified. There remains the possibility that the lot from India is actually identical with the genotype, *ferox* Newstead, and that the lot from Java is the species described by Vayssière as *Aspidoproctus serrei* (*166, p. 334*). In the absence of positive evidence on these points no attempt is made here to separate the species actually studied.

Genus Pseudaspidoproctus Morrison

(Pl. 4, C, and figs. 66 and 67)

This genus has just been established by the writer (*136, p. 104*) for the reception of several African species belonging in the tribe Monophlebini.

GENERIC CHARACTERISTICS

Habit.—Living exposed on the host plant during the growing period; eggs deposited within an internal marsupium having a U-shaped or V-shaped opening.

Adult female.—Of moderate size (about 7 mm.), elliptical, strongly convex above, flattened beneath, with some pulverulent secretion; as mounted broadly elliptical, derm not definitely chitinized; antennae variable, 8-segmented to 11-segmented, tapering, basal segment large, terminal one slender, elongate, sensory setae not sharply differentiated; legs stout, some of setae on under sides of femur, tibia, and tarsus stout, spinelike, claw stout, somewhat curved, the inner face often roughened to almost denticulate, the digitules stout at base, with slender tips not attaining apex of claw; beak short, stout conical, obscurely three-segmented, the apical sensory setae acute at tips; thoracic spiracles large, but not conspicuous, with bar but no cluster of pores at opening; abdominal spiracles much smaller, with thickened rim, inconspicuous, in seven pairs; derm pores small, inconspicuous, centers circular, triangular, quadrilocular, with five to six outer loculi, these often indistinct, some, in the ventral marsupial area, larger, with circular center and about nine loculi; derm spines numerous, but not densely crowded, not arranged in definite groups or clusters, of two sorts, one slightly curved, cylindrical or very slightly clavate with bluntly rounded tips, the other larger, tapering with expanded bases, and tips rounded or pointed, the first confined to the dorsum, the second present on both surfaces, more abundant ventrally; hairs, as here considered, few, apparently confined to the invaginated marsupium; setae fairly numerous, stout, but not long, relatively conspicuous, larger along body margin; anal tube short, hardly as deep as wide, with a row of wax pores at inner end, somewhat chitinized, the opening surrounded by a cluster of spines and setae, but these not in a definitely differentiated cluster; ventral cicatrices three in number, placed close together approximately beneath anal tube, elongate to very elongate, usually more or less irregular in shape.

Intermediate female.—In general resembling the adult female; smaller, with fewer antennal segments, setae, hairs, and pores much fewer in number, spines of the cylindrical type most abundant, although not crowded.

Larva.—As mounted, elliptical or somewhat ovate, broadest anteriorly; antennae five-segmented, slender, elongate, third and apical segments much longer, one apical seta fairly long, the remaining antennal setae short, some sensory setae differentiated; legs long, of average stoutness, claw slender, somewhat curved, claw digitules approaching but not attaining claw apex; beak indistinctly two-segmented, short stout conical, the apical sensory setae somewhat pointed at tips; thoracic spiracles large, with bar and a single disk pore near opening; abdominal spiracles in seven pairs, relatively minute, simple tubular; derm pores of two sorts, one, in longitudinal rows dorsally and ventrally, normally with trilocular center and usually three loculi, the other, near

thoracic spiracles and in and around anal tube, multilocular with circular to triangular center and usually six loculi; cylindrical derm spines numerous, in marginal, median, and intermediate longitudinal dorsal bands; derm hairs few, small, perhaps confined to a submarginal row; derm setae numerous, varying greatly in size, of moderate size ventrally, some, along margin and in median

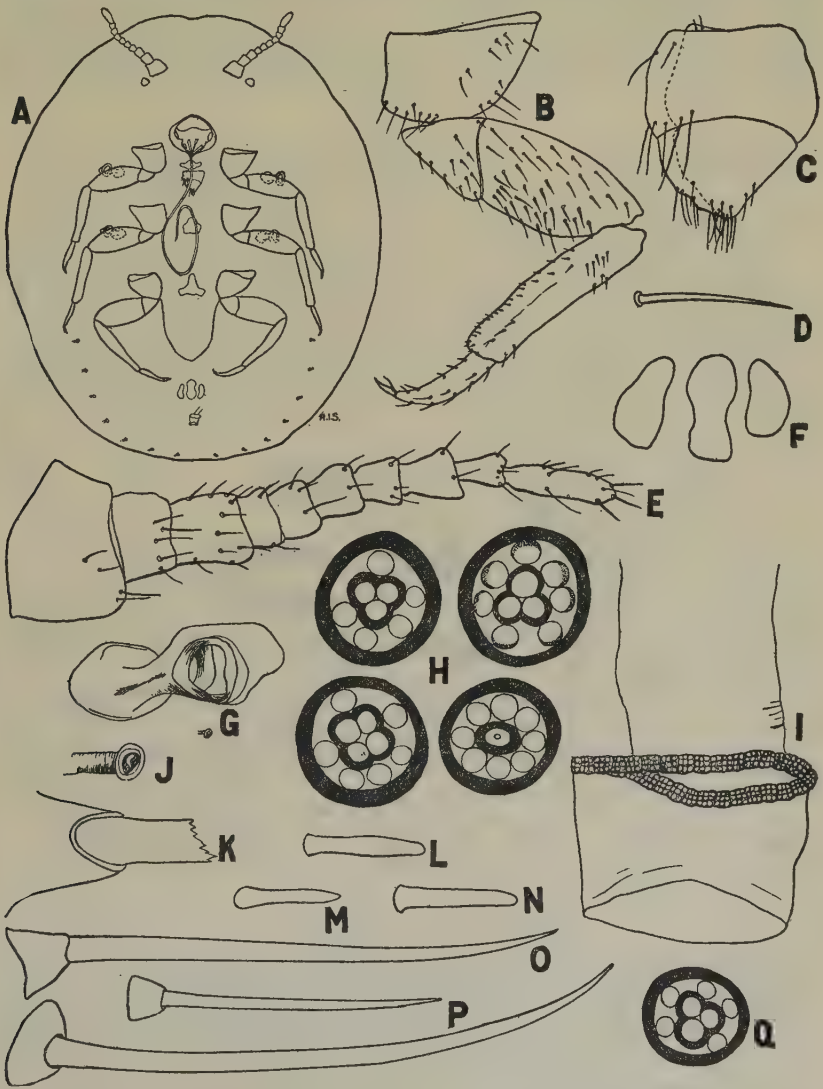

FIG. 66.—*Pseudaspidoproctus hyphaeniacus*, adult female: A, outline, optical section, × 7.5; B, leg, × 30; C, beak, × 60; D, sensory seta from beak, × 230; E, antenna, × 60; F, ventral cicatrices, × 30; G, thoracic and abdominal spiracles, × 60; H, middorsal derm pores, × 1,500; I, anal tube, × 165; J, abdominal spiracle, × 230; K, base of largest type marginal seta, × 650; L, ventral derm spine, × 650; M, middorsal derm spine, × 650; N, marginal derm spine, × 650; O, dorsal seta, × 650; P, ventral setae, × 650; Q, ventral disk pore, × 1,500

paired, intermediate, and marginal single rows dorsally, relatively large, some, at least, of the marginal approaching the apical pair in size and length; anal tube of moderate length, with a double row of wax pores at inner end and a ring of multilocular disk pores near inner end, and another scattered circle of these

pores well outside the opening, anal opening with a half circle of six setae with slightly flattened and fimbriate tips; with a single median, ventral cicatrix, often irregular in outline.

Adult male (based only on Brain's (*3, p. 162*) description of *fulleri* male).—Elongate, apex of head triangular in outline; antennae with the segments beyond the third nearly cylindrical or somewhat irregular but not distinctly nodose, and with the setae not in whorls, but scattered, the apical segment approximately as long as the preapical; halteres small, flattened, with a few (perhaps four or five) long, curved, knobbed, apical setae; apex of abdomen with two very long fleshy tassels; penis sheath stout, tapering about uniformly, broad and bluntly rounded at apex.

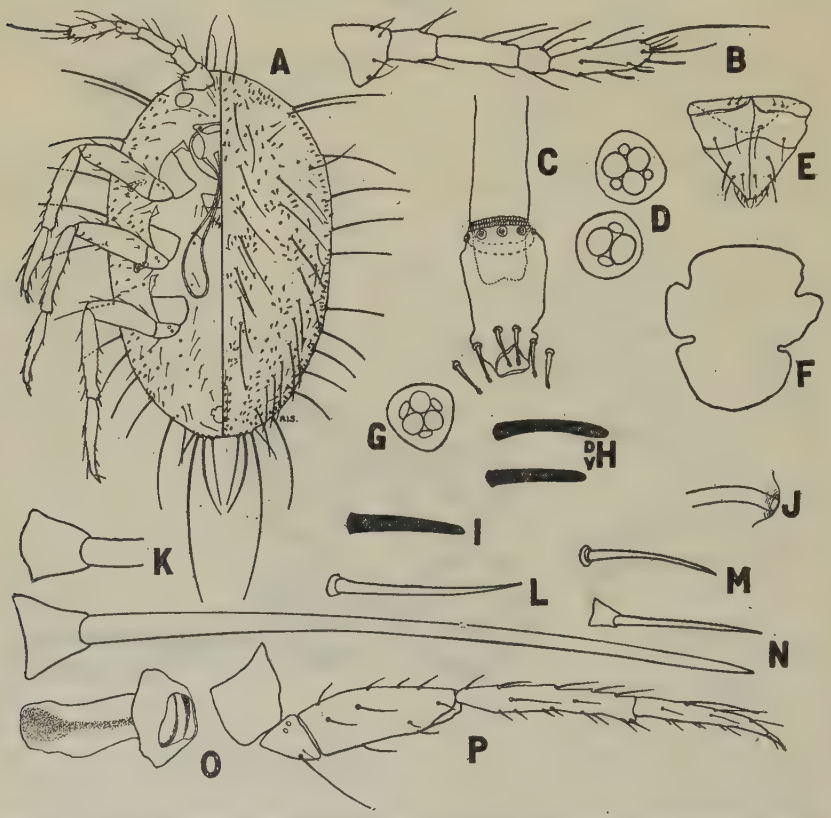

FIG. 67.—*Pseudaspidoproctus hyphaeniacus,* larva: A, outline, dorsal and ventral, × 60; B, antenna, × 115; C, anal tube, × 330; D, ventral disk pores, × 1,500; E, beak, × 115; F, ventral cicatrix, × 330; G, dorsal derm pores, × 1,500; H, marginal spines, dorsal (D) and ventral (V), × 650; I, middorsal spine, × 650; J, abdominal spiracle, × 1,500; K, base of large apical seta, × 650; L, midventral seta, × 650; M, lateral dorsal seta, × 650; N, middorsal setae, × 650; O, thoracic spiracle, × 115; P, leg, × 115

The type of this genus is the species described as *Aspidoproctus hyphaeniacus* Hall (*85, p. 1*). In addition, the species *Monophlebus fulleri* Cockerell (*21, v. 34, p. 223*) and *Walkeriana africana* Newstead (*145, p. 3*) are definitely included here. On the assumption that Cockerell's indication of close relationship between it and *fulleri* is accurate, then *Monophlebus fortis* Cockerell (*21, v. 34, p. 224*) should also be assigned here. *Monophlebus acaciae* Joubert (*101a, p. 119*) is said to be closely related to *fulleri* and may also belong here.

Finally, it seems possible that *Perissopneumon zimmermanni* Newstead (*148, p. 157*) may also belong with these species.

The distribution, so far as known, includes certain portions of the African continent.

From the fragmentary information given by Brain (*3*) regarding collection dates when certain stages of *fulleri* were obtained, it seems probable that the species of this genus have one generation annually, with active growth during the summer months.

GROUP 2

If the evidence from the specimens of various species available for study may be accepted as a positive indication of the characteristics possessed by all species assigned here, then this group of genera and species is apparently a natural one, although of uncertain value.

The characteristics which separate this group from the preceding, again on the basis of available material, include, in the first-stage larva, the presence along the body margin of large bilocular tubular pores producing straight threads of glassy secretion; and, in the adult female, the persistance of a few of these large tubular pores (one apparent exception).

Genus Walkeriana Signoret

(Pl. 4, D, and figs. 68 and 69)

This genus was erected by Signoret (*158, p. 390*) in 1875 for the species described from Ceylon by Walker (*171, p. 305*) as *Coccus floriger*. Some species from Africa and additional ones from Ceylon have been added from time to time. Certain of the African species have been transferred elsewhere. The status of others remains uncertain. New genera have been established for some of the species from Ceylon. At present only a few species from the island of Ceylon are definitely included in the genus.

GENERIC CHARACTERISTICS

Habit.—Living on the bark of the host; eggs deposited beneath body of female.[26]

Adult female.—Externally covered densely with secretion arranged in definitely formed tufts and masses; broadly elliptical, convex above, flattened or concave beneath, shape of mounted specimens similar to those of unmounted; derm membranous, but densely crowded with spines dorsally; antennae normally 10-segmented, the terminal longest, but narrowest, with setae numerous, but the sensory setae not sharply differentiated from the remainder; legs stout, some of setae on under sides of femur, tibia, and tarsus stout, spinelike, claw stout, curved, digitules uncertain; beak very short conical, one-segmented, the apical sensory setae acute at tips; thoracic spiracles large, with bar, with a tendency toward the formation of a pore cluster at mouth; abdominal spiracles of fair size, very short wrinkled cylinders, but inconspicuous because concealed in the midst of dense clusters of spines, believed to be in seven pairs, but not more than six pairs definitely recognized in any one specimen; derm pores numerous and, in general, large, with heavily chitinized borders, but varying extensively in size and extent of chitinization, in three general types, multilocular disk, with from 6 to about 11 loculi, this type very numerous ventrally and around anal opening, with quadrilocular disk pores, these more

[26] This generic characterization probably will not hold for *W. senex* Green, in which an ovisac is developed.

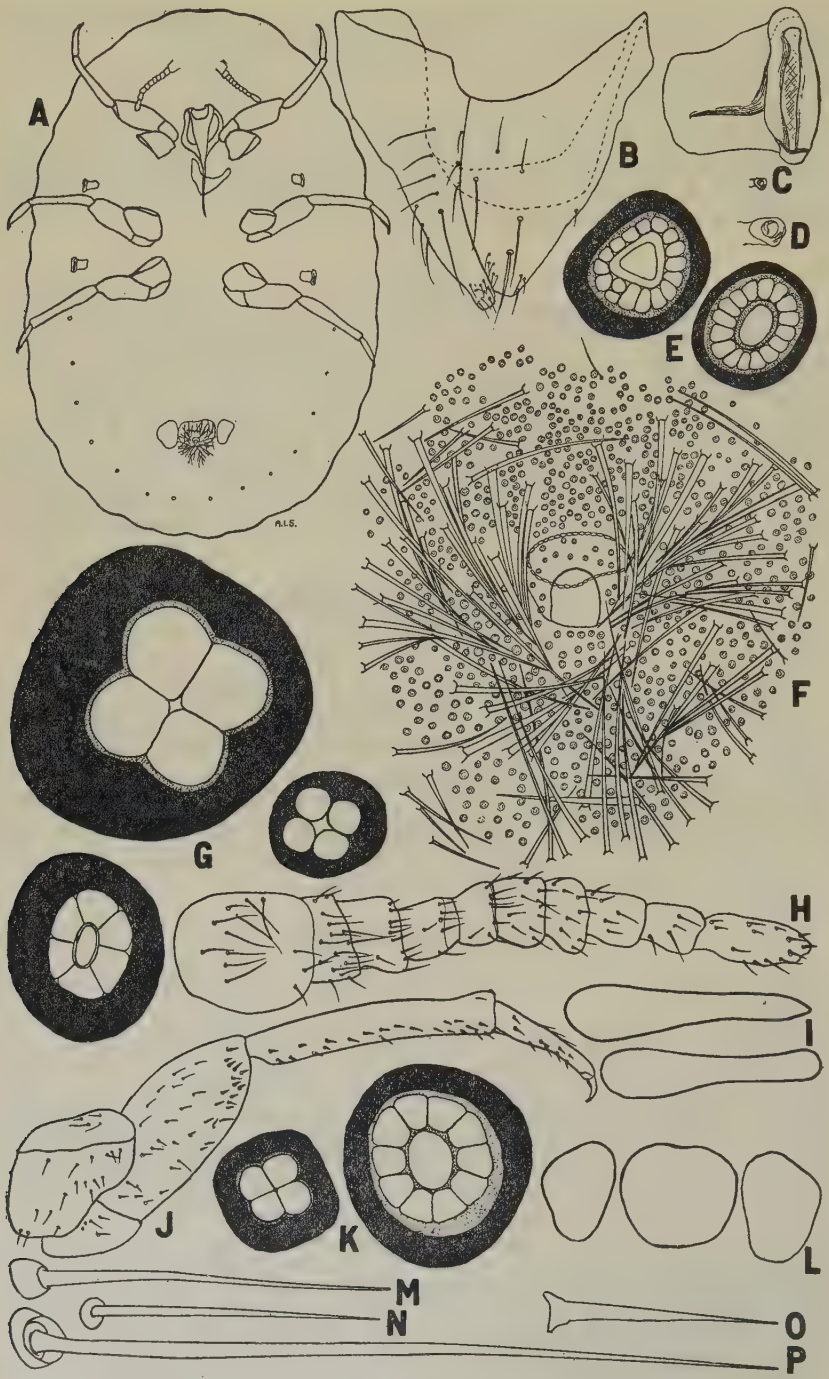

FIG. 68.—*Walkeriana floriger*, adult female: A, outline, × 7.5; B, beak, × 60; C, thoracic and abdominal spiracles, × 60; D, abdominal spiracle, × 120; E, disk pores from anal area, × 1,500; F, anal area, × 165; G, dorsal disk pores, × 1,500; H, antenna, × 60; I, dorsal spines, × 650; J, leg, × 50; K, ventral disk pores, × 1,500; L, ventral cicatrices, × 60; M, ventral seta, × 650; N, dorsal seta, × 650; O, ventral spine, × 650; P, dorsal seta, × 650

abundant dorsally, and with large tubular bilocular pores in small clusters along body margin; derm spines very abundant and closely crowded dorsally and at margins, all of those present dorsally swollen at bases, some, in clusters outlined by rows of gland pores, with the apices somewhat swollen, others, placed between these clusters, with the apices tapering to points; ventral surface with some hairs, many apparently setalike spines, and a number of setae, these last with almost cylindrical basal collars varying considerably in size and also occurring dorsally; anal tube not particularly chitinized, with a row of polygonal wax pores at inner end, tube opening externally in the center of a cluster of multilocular disk pores and long stout setae; with

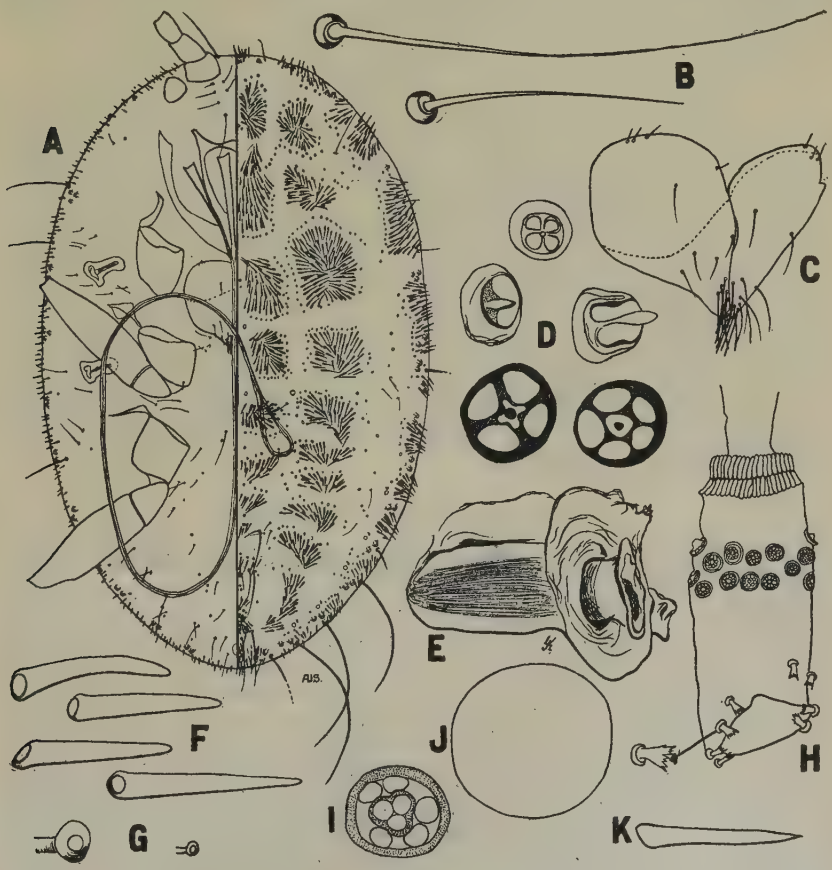

FIG. 69.—*Walkeriana floriger*, larva: A, outline, dorsal and ventral, × 60; B, derm setae, × 650; C, beak, × 115; D, derm disk pores, surface and section, × 1,500; E, thoracic spiracle, × 460; F, derm spines, × 650; G, abdominal spiracle, to right × 460, to left × 1,500; H, anal tube, × 330, with detail of seta, × 650; I, ventral derm pore, × 1,500; J, ventral cicatrix, × 330; K, acute-tipped dorsal spine, × 650

three oval to nearly circular ventral cicatrices located close together approximately below the anal tube.

Larva (based on genotype only).—Body elliptical; derm not chitinized, but with numerous spine clusters; antennae stout, five-segmented; legs rather large, characters uncertain because of breakage; beak stout conical, one-segmented, the sensory setae bluntly pointed at apices; thoracic spiracles large, with bar, and usually with a single quadrilocular disk pore at mouth; abdominal spiracles much smaller, inconspicuous, presumably in seven pairs, although only six have been located definitely thus far, each placed near to, but not necessarily intimately associated with, a quadrilocular disk pore; derm pores of three types, quadrilocular, with number of loculi varying from three to six, dis-

tributed over both surfaces, multilocular, usually with about 9 to 11 loculi, distributed ventrally and in the anal region dorsally, and large bilocular tubular, placed singly or in pairs along the body margin; spines numerous, arranged in definite marginal, median, and intermediate dorsal clusters, most of these incompletely outlined by single rows of small quadrilocular disk pores, general shape of spines stout, tapering somewhat and bluntly rounded or pointed at tips; body hairs occurring ventrally, few, small, inconspicuous; body setae mostly small and slender, apical much enlarged, some additional along body margin likewise much enlarged, perhaps half length of apical, all with nearly cylindrical to rather long conical collars; anal tube rather long and large, the inner end with a double row of polygonal wax pores, a double row of multilocular disk pores about the middle, and a circle of the short fimbriate-tipped setae around the opening, and outside these another circle of multilocular disk pores; with a single circular median ventral cicatrix.

As now limited, the genus is confined to the island of Ceylon.

There appears to be no definite information of any sort available in regard to the biology of the included species. They live normally on the woody tissue of the host plant and it has been suggested by Green that they are probably long-lived and slow in development.

The species definitely included in this paper are *floriger* (Walker), *compacta* Green, and *ovilla* Green. The species *senex* Green is also assigned here by Green in his recent excellent and detailed treatment of the genus (*65*, *p. 444*), but in the view of the writer it should be excluded because of the development of an ovisac band and an ovisac. This treatment by Green of the species of Walkeriana is so much superior to anything that can be produced from the study of the very few specimens of the included species which are available that no attempt is made here to offer keys to, or further notes on, the included species.

Genus Monophlebus Burmeister

This genus, the first to be characterized within the subfamily, contained two species as originally described (*5*, *p 80*, *81*), one, *atripennis* from Java, known only from the adult male, the other, *fuscipennis* from Germany, known from both adult female and adult male. Signoret (*158*, *p. 359*) in 1875 removed the species *fuscipennis*, which he placed in his genus Leachia along with *Monophlebus brasiliensis* Walker. No type citation for either of these genera appears to have been made prior to 1902, although Cockerell (*8*, *p. 36*) in 1894 called attention to the prior use of Leachia for another genus of animals and substituted for it the name Palaeococcus. The type for the genus appears to have been definitely fixed by Cockerell (*23*, *p. 232; 24*, *p. 317*) in two articles published in 1902, when he designated the species *atripennis* Klug of Burmeister as type, this species in reality standing as *atripennis* Burmeister.

The actual status of the species remains uncertain even to-day, as it has never been definitely rediscovered. From a study of the original description, it is the belief of the writer that the species and genus may be correctly located among the forms including Walkeriana and closely related genera. The original description implies the occurrence of antennae having trinodose segments beyond the second; it definitely describes the abdomen as terminating in a single pair of fleshy tassels, and the insect as described is fairly large in size (3½ lines=about 7 mm.). There remains a possibility that the species really represents a male of the genus here designated as

Drosicha, as the deep incisions described for the margins of the abdomen may perhaps actually represent the spaces between imperfectly developed lateral marginal tassels. Because of uncertainty as to the characters of the species described by Fabricius (*45, p. 46*) as *Chironomus dubius* it has been left in this genus without a critical expression of opinion.

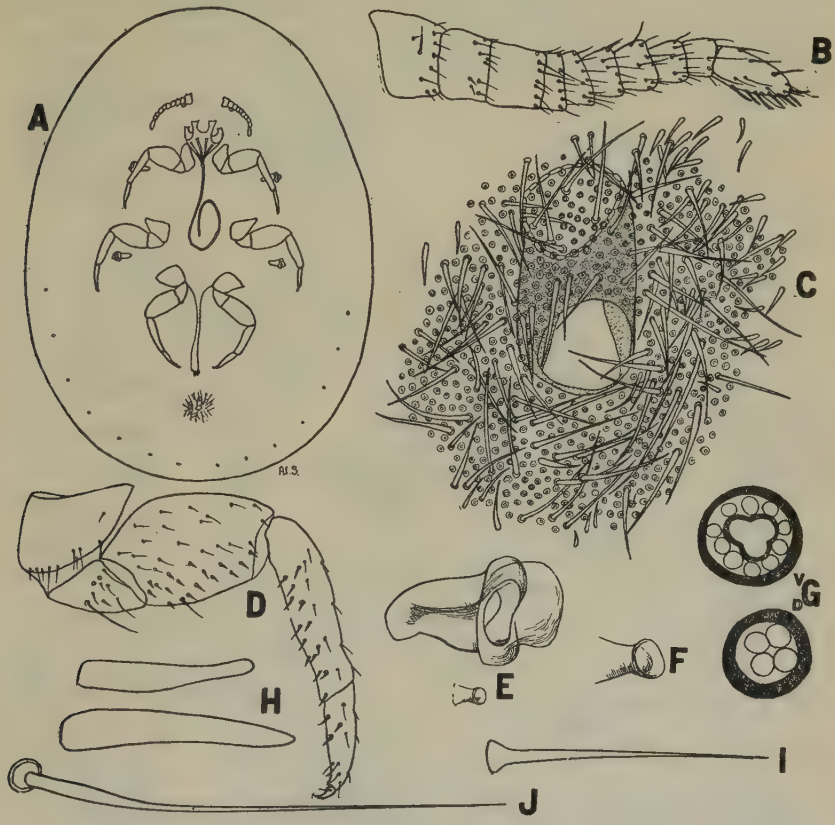

FIG. 70.—*Labioproctus poleii*, adult female: A, outline, optical section, × 7.5; B, antenna, × 60; C, anal area, × 115; D, leg, × 30; E, thoracic and abdominal spiracles, × 60; F, abdominal spiracle, × 120; G, ventral (V) and dorsal (D) derm disk pores, × 1,500; H, dorsal spines, × 650; I, ventral hair, × 650; J, body seta, × 650

GENUS LABIOPROCTUS GREEN

(Pl. 4, E, and figs. 70, 71, and 72)

This genus was established by Green (*65, p. 453*) in 1922 for a species first described by him many years before (*64, p. 6*) but previously assigned to Walkeriana. Thus far no species other than the genotype, *Walkeriana poleii*, has been assigned here.

GENERIC CHARACTERISTICS

Habit.—Living exposed on the twigs of the host; eggs deposited within an internal marsupium.

Adult female.—In life (according to Green) oblong oval, strongly convex, bearing marginal and dorsal tufts of dense secretion, but with very little

secretion between the tufts; as mounted rather broadly elliptical, of moderate length (about 8 mm.); derm becoming more or less chitinized at full maturity; antennae normally 10-segmented, stout, tapering gradually, the apical segment longest, the margins of the intermediate and apical segments bearing definitely differentiated, enlarged sensory setae; legs stout, sparsely provided with setae, some of those on the under sides of trochanter, femur, tibia, and tarsus very stout, spinelike, claw stout, fairly strongly curved, claw digitules slender toward tips, probably approaching the tip of the claw; beak very short conical, one-segmented, the apical sensory setae tapering; thoracic spiracles large, without pore cluster at opening; abdominal spiracles small, simple, inconspicuous, number of pairs not absolutely determined but believed to be seven, situated

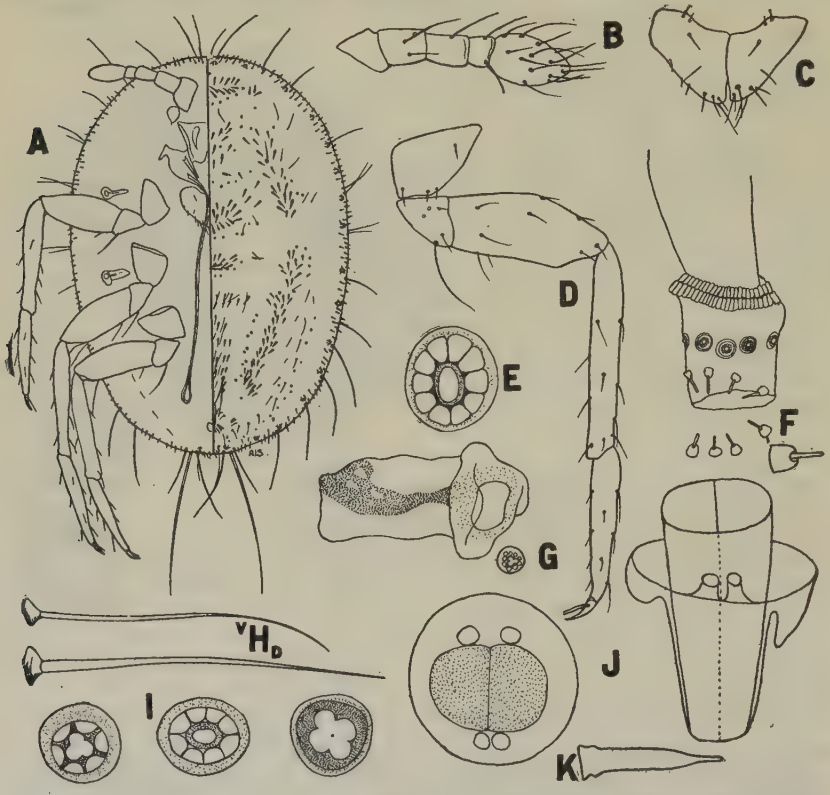

FIG. 71.—*Labioproctus polelii*, larva: A, outline, dorsal and ventral, × 60; B, antenna, × 115; C, beak, × 115; D, leg, × 115; E, disk pore from anal tube, × 1,500; F, anal tube, × 330, with detail of seta, × 650; G, thoracic spiracle, × 460; H, derm setae, ventral (v) and dorsal (D), × 650; I, derm disk pores, three sorts, × 1,500; J, large marginal bilocular tubular pore, face and side, × 1,500; K, derm spine, × 650

dorsally; derm pores not so greatly enlarged as in Walkeriana, with a few large bilocular tubular pores at the edge of the body adjacent to the clusters of specialized spines, with some more heavily chitinized, quadrilocular disk pores in and near the spine clusters over the dorsal surface and in rows outlining the spine cluster supporting the secretionary tufts, with a large cluster of larger, lightly chitinized disk pores, circular with roughly circular centers and 9 to 16 loculi around genital opening, and with rather lightly chitinized pores of medium size with circular, triangular, or oval centers and about nine loculi scattered over the ventral surface and to a lesser extent dorsally; body spines numerous, the normal dorsal type stout, slightly curved, tapering from a slight swelling near base to a bluntly pointed tip, those serving as bases for the secretionary tufts, both dorsal and marginal, quite characteristic, swollen near

base, then nearly cylindrical, then somewhat swollen again near tip; acutely conical spines present in the midventral area, these apparently more slender in early adult female stages; with some hairs in the midventral area between

FIG. 72.—*Labioproctus poleii*, adult male: A, head, dorsal, × 60; B. third antennal segment, × 60; C, derm disk pores, × 1,500; D, posterior apex of abdomen, showing only one apical fleshy tassel, × 60; E, antenna, × 30; F, halter, × 120; G, tubercle from apex of abdomen, × 1,500; H, tarsus and claw, × 120; I, abdominal spiracle, × 530; J, leg, × 30; K, ventral abdominal seta, × 650; L, dorsal abdominal seta, × 650; M, submarginal, dorsal, abdominal seta, × 650

and around legs and on each side of marsupial slit, these of the usual form, slender, with expanded base; derm setae slender, inconspicuous, present both dorsally and ventrally, with cylindrical or slightly conical collars; anal tube

cylindrical, distinctly chitinized, with a single row of polygonal wax pores at inner end, tube opening in the midst of a cluster of multilocular disk pores and large setae; ventral cicatrices not located with absolute certainty, but apparently three in number, elongate, narrow, placed precisely at the posterior termination of the slitlike marsupial opening, and so actually on a somewhat curved dorso-ventral axis rather than on the usual horizontal one.

Larva.—Elliptical; derm not chitinized; antennae five-segmented, the terminal largest, swollen, bearing stouter sensory setae as well as the ordinary slender sort; legs long, the trochanter with two sensory pores on each face, claw with two distinct denticles, claw digitules exceeding tip of claw; beak very stout conical, one-segmented, the sensory setae at apex pointed at tips; thoracic spiracles large, with bar, and with a single pore behind mouth; abdominal pairs not certainly located, evidently minute; margin of body with quite large, bilocular tubular, ductlike pores, derm with quadrilocular disk pores in longitudinal rows, with disk pores normally with triangular centers and 6 loculi and, within anal tube and around the opening, with approximately circular disk pores having about 11 loculi; derm bearing stout spines in five rows dorsally, median, two intermediate, and two marginal; body hairs present both dorsally and ventrally, few in number, long and slender; with body setae evident, but not particularly conspicuous, some along the body margin, between the antennal bases and anterior to the anal opening, longer than the average, and quite evident, only the apical pair of marginal setae strongly developed, but even these not more than one-fourth or one-third the length of the body, the longer of the remaining marginal abdominal setae about half or less than half the length of the apical pair, but quite conspicuous compared with Aspidoproctus; anal tube somewhat chitinized, with a double band of polygonal wax pores at inner end, an intermediate ring of circular multilocular disk pores, and a row of short, blunted or sometimes fimbriate setae around the apex, as in Aspidoproctus; with a single, median, circular, ventral cicatrix.

Adult male.—Of the usual elongate shape, abdomen in particular rather slender, apex of head triangular in outline; antennae slender, the intermediate segments each more or less distinctly trinodose and with the setae tending to cluster in three groups but definitely not forming distinct whorls of setae, apical and preapical segments approximately equal in length; wings heavily infuscated, the veins as usual for the subfamily, the basal diagonal extending about two-thirds to three-fourths of the distance to the margin; legs slender, trochanters with two sensory pores on each face, anterior femora without bifurcate setae, claw definitely curved, without denticles, digitules slender, probably not surpassing apex of claw; abdomen without chitinized plates, derm bearing elongate slender setae and the usual quadrilocular disk pores in transverse rows on both surfaces; probably, but not wholly certainly, with seven pairs of quite evident, though only lightly chitinized, abdominal spiracles; abdomen with a single pair of elongate, apical, fleshy tassels; penis sheath of moderate width at base, tapering, terminal section slender, nearly cylindrical, ventral valve short.

As previously stated, the only species thus far included here is the genotype, *Labioproctus poleii* (Green), known from Ceylon, Java, and south India. No information regarding biology and habits appears to be available.

Genus Hemaspidoproctus Morrison

(Pl. 4, F, and figs. 73 and 74)

This genus has just been established by the writer (*136, p. 104*) for two species from Ceylon and India that were assigned to the genus Aspidoproctus by Green (*65, p. 450*). The writer considers it possible that *Walkeriana senex* Green may be assignable here, but such assignment can not be made definite.

GENERIC CHARACTERISTICS

Habit.—Living exposed on the stems and leaves of the host plants; eggs deposited in a large half-marsupium formed in the ventral abdominal area, and covered over by a secretionary pad.

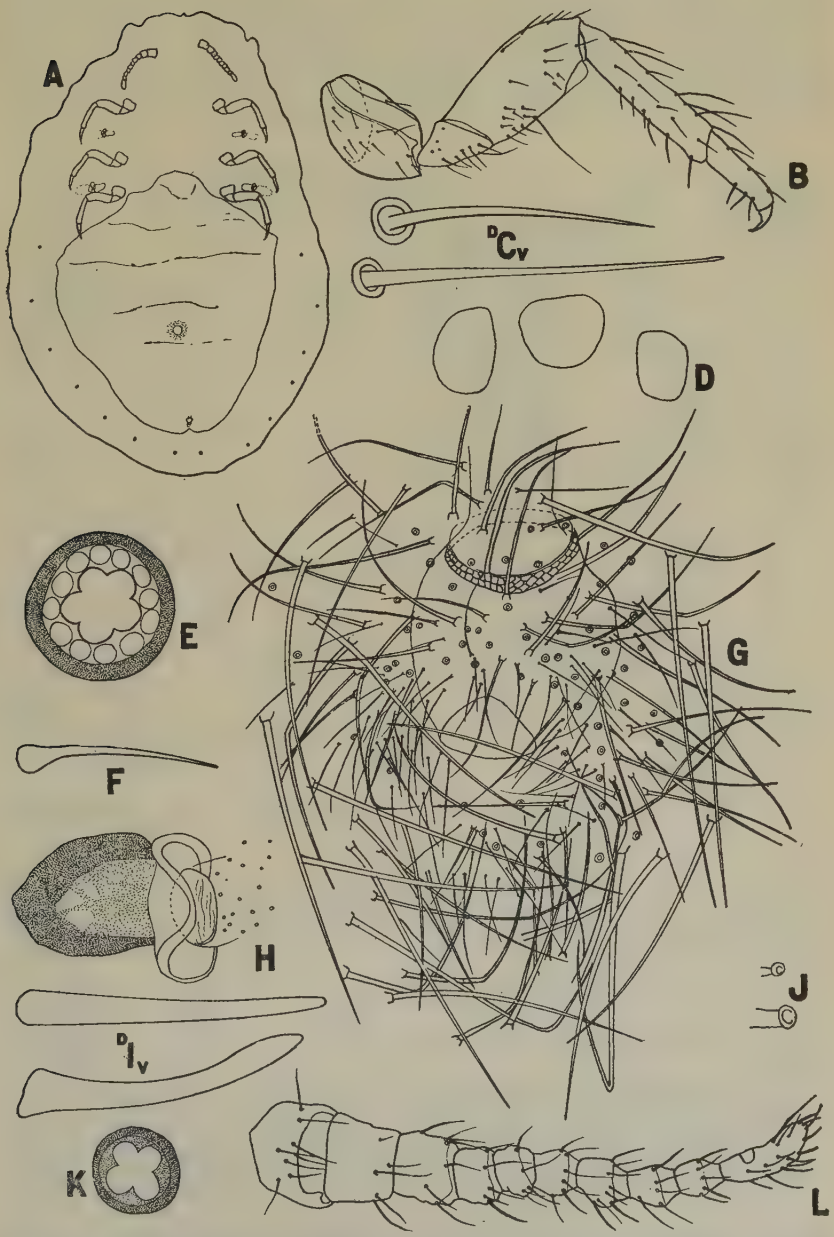

FIG. 73.—*Hemaspidoproctus cinereus*, adult female: A, outline, optical section, showing outline of marsupial opening, × 7.5; B, leg, × 50; C, derm setae, dorsal (D) and ventral (V), × 650; D, ventral cicatrices, × 40; E, ventral derm disk pore, × 1,500; F, ventral derm hair, × 650; G, anal area with tube, × 80; H, thoracic spiracle, × 60; I, derm spines, dorsal (D) and ventral (V), × 650; J, abdominal spiracle, above × 60, below × 120; K, dorsal derm disk pore, × 1,500; L, antenna, × 60

Adult female.—Body ovoid, broader and strongly convex behind, with a thin layer of secretion and rows of protruding secretionary tufts dorsally; as mounted, more or less distinctly ovoid; derm with a semicircular or half-elliptical narrow chitinized band around the under side of the abdomen; antennae normally 10-segmented, tapering somewhat, the apical segment longest, the sensory setae definitely differentiated; legs moderately stout, the setae on the under sides of the parts not spinelike, claw stout, somewhat curved, claw digitules probably not attaining claw apex; beak short conical, two-segmented,

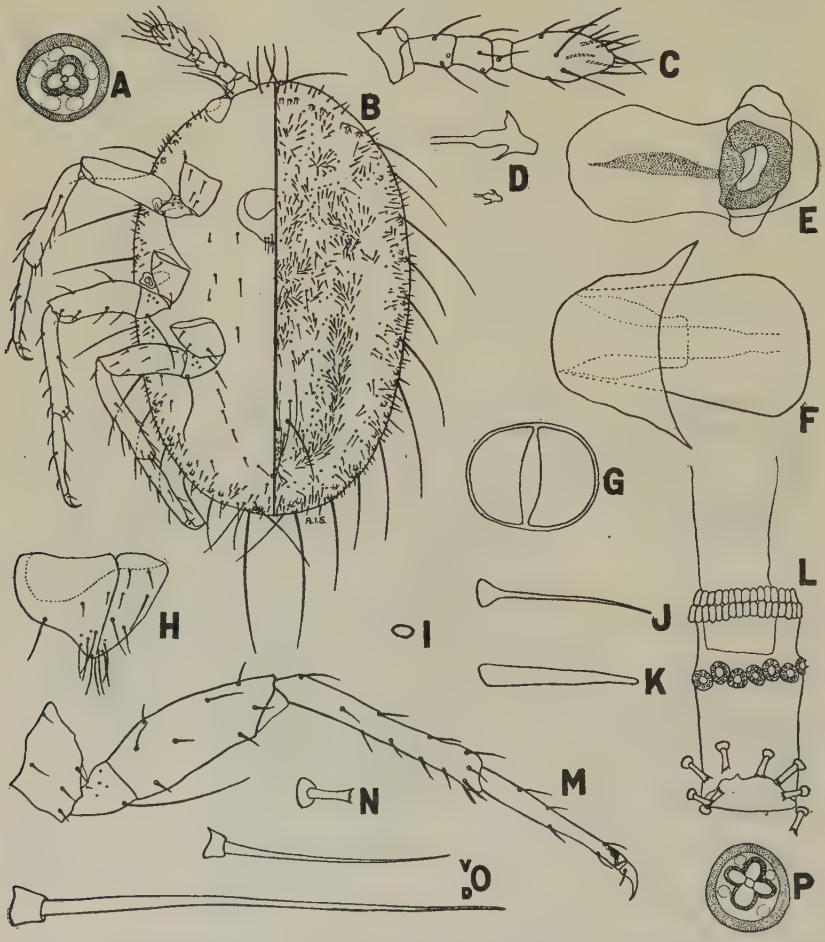

FIG. 74.—*Hemaspidoproctus cinereus*, larva: A, derm disk pore from apex of abdomen, × 1,500; B, outline, dorsal and ventral, × 60; C, antenna, × 115; D, abdominal spiracle, above × 1,500, below × 460; E, thoracic spiracle, × 460; F, large marginal bilocular tubular pore, side, × 1,500; G, same, surface view, × 1,500; H, beak, × 120; I, ventral cicatrix, × 330; J, dorsal hair, × 650; K, dorsal spine, × 650; L, anal tube, × 330; M, leg, × 115; N, seta near anal opening, × 650; O, derm setae, dorsal (D) and ventral (V), × 650; P, middorsal derm disk pore, × 1,500

the apical sensory setae pointed at tips; thoracic spiracles large, with bar, without a distinct pore cluster at opening; abdominal spiracles in seven pairs, much smaller than thoracic, but fairly evident, placed dorsally; derm pores varying in size, moderately heavily chitinized, showing considerable variation in number and arrangement of the loculi, the quadrilocular type, often deep and tubular in form, predominating, and in addition forming the band of pores around the venter of the abdomen and particularly across the anterior margin, producing the rudimentary ovisac; large, bilocular, tubular pores apparently

not persisting in adult; derm spines most abundant in crowded clusters serving as bases for the secretionary tufts, rather scattered elsewhere, present dorsally and ventrally to margin of ovisac band, all with somewhat swollen bases and bluntly pointed tips; hairs rather numerous between the legs, present, but few in number, over the ventral abdominal area; derm setae fairly numerous, slender, rather small, except for a cluster of large setae around anal opening; anal tube stout, with double row of wax pores at inner end, the opening surrounded by a cluster of large setae; with normally three to five approximately circular ventral cicatrices of moderate size arranged in a curved row behind genital opening.

Larva.—Closely resembling the larva of Aspidoproctus in most particulars; the dorsal spines in longitudinal rows, not in clusters as with Walkeriana; antennae five-segmented, short and stout, bearing short setae; legs of moderate length, not unusual; beak uncertain from material available; thoracic spiracles with bar; abdominal spiracles minute, probably in seven pairs; derm pores of three sorts, quadrilocular disk, multilocular disk with trilocular center and usually three additional small loculi, and large marginal bilocular tubular; derm spines numerous, in marginal, intermediate, and median dorsal rows; derm hairs few, inconspicuous, apparently confined to venter; derm setae fairly numerous, small ventrally, much larger along the margin and the middorsal line, but in no case very long or conspicuous, the apical pair little, if any, longer than some of dorsal setae, and but little longer than other marginal setae; anal tube short, with double row of wax pores at inner end, a ring of disk pores near inner end, a circle of special setae outside of opening and a scattered ring of disk pores around these; apparently with a single, circular, median, ventral cicatrix.

Adult male.—Not known.

The present known distribution includes Ceylon and India.

There is no published information regarding the life cycle of the included species.

This generic diagnosis has been drawn up from specimens of the genotype, *W. cinerea*, from Ceylon, received from Green, from specimens of the same from India, and from specimens of the other included species, originally described as *Walkeriana euphorbiae*, also from Ceylon and received from Green.

Genus Aspidoproctus Newstead

(Pl. 5, A, B, C, D, and figs. 75, 76, 77, 78, and 79)

The generic name Aspidoproctus was first proposed in 1900 by Newstead (*143, p. 948*), with the species *pertinax* as type, although no such intention was in view at the time, since it was definitely stated that the characters once regarded as of generic rank were later considered to be specific only. However, since the International Code of Nomenclature appears to make no allowance for the intent of the author at the time of publication, and since the conditions under which Newstead published the name conform fully with those set forth in article 25 of this code, there appears to be no latitude with respect to its acceptance and utilization. Cockerell (*21, v. 34, p. 227*) described the genus Lophococcus, based on *mirabilis*, a species similar to Newstead's *pertinax* in anatomical characters, during the year following and definitely announced its generic standing at the time. Subsequent writers have alternated between the two names as they considered one or the other valid, or as they considered that the two actually represented distinct and valid genera. Brain (*3, p. 175*) and Vayssière (*168, p. 428*) have already definitely indicated the identity of Aspidoproctus and Lophococcus.

GENERIC CHARACTERISTICS

Habit.—Living on the branches and twigs of the host; eggs deposited within a large internal marsupium having a small midventral opening normally covered by a flap of secreted material.

Adult female.—Size large to very large (10 to 33 mm.), early adult female usually flattened, with solid marginal tufts of dirty white secretion and the dorsal surface nodulose or with prominent projecting ridges or spikes, surface

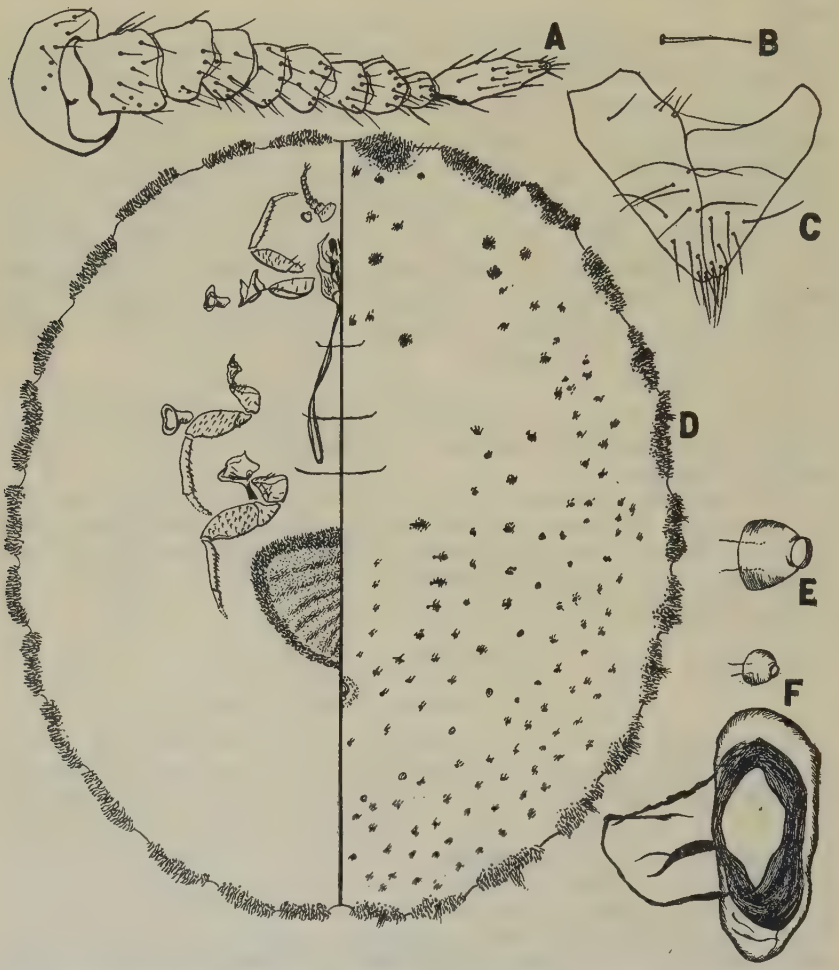

FIG. 75.—*Aspidoproctus maximus,* early adult female: A, antenna, × 60; B, sensory seta from beak, × 120; C, beak, × 60; D, outline, dorsal and ventral, × 7.5; E, abdominal spiracle, × 120; F, abdominal and thoracic spiracles, × 60

usually coated with a thin layer of grayish wax pubescence; fully matured adult female with the whole dorsal derm fairly heavily chitinized and dark in color; the body proper much distended dorso-ventrally or in all dimensions and the marginal tufts and dorsal wax pubescence usually much mutilated or wanting, ventral surface thickly coated with whitish wax; body outline, in general, short elliptical, the longitudinal or cross section varying according to the modifications of the various species; antennae normally 10-segmented, the apical segment longest, the intermediate wider than long, the sensory setae not sharply differentiated; legs large, stout, the setae not numerous, those along ventral

face of tibia and tarsus stout, spinelike, trochanter with two or more sensory pores on each face, claw stout, digitules not attaining apex of claw; beak very short conical, one-segmented or, at most, very obscurely two-segmented, the apical sensory setae acute at tips; thoracic spiracles large, with broad bar, without definite pore band or cluster at opening; abdominal spiracles in seven

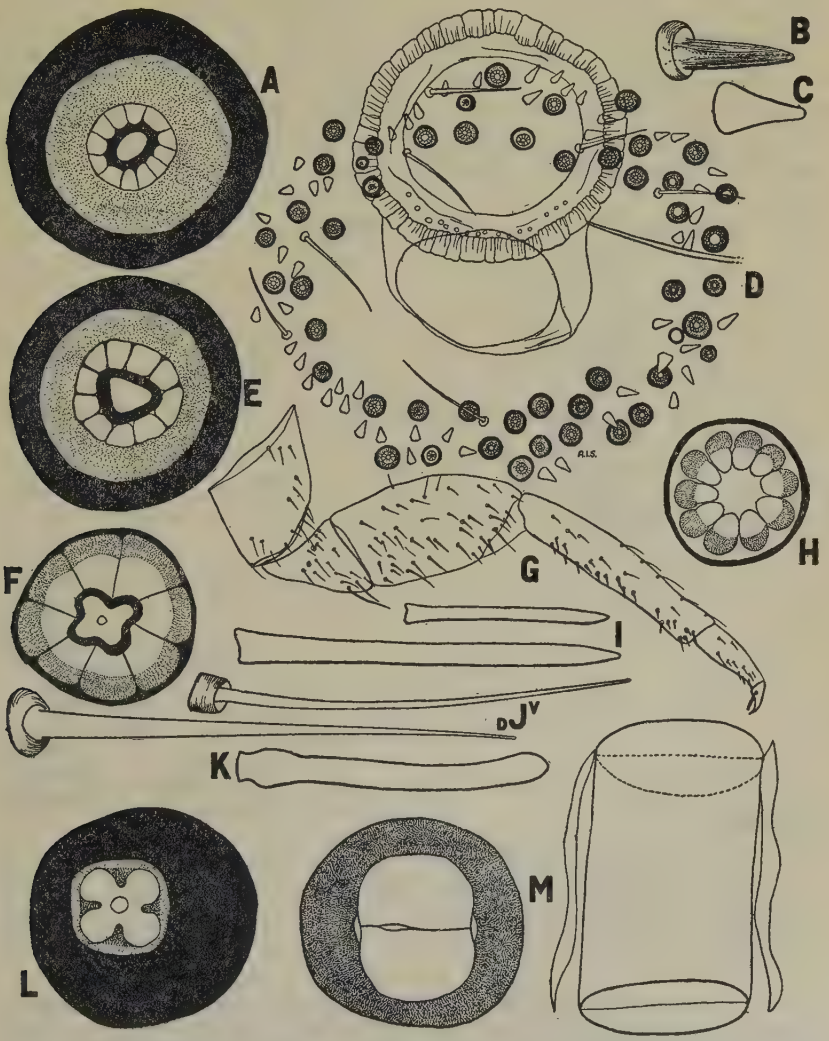

FIG. 76.—*Aspidoproctus maximus*, adult female: A, disk pore from anal area, × 1,500; B, dorsal spine, × 650; C, anal area spine, × 650; D, anal area, × 165; E, dorsal derm disk pore, × 1,500; F, ventral derm disk pore, × 1,500; G, leg, × 26.5; H, midventral derm disk pore, × 1,500; I, midventral thoracic spines, × 650; J, setae from ventral (V) marsupial and dorsal (D) anal areas, × 650; K, lateral marginal cylindrical spine, × 650; L, quadrilocular derm disk pore, × 1,500; M, large marginal bilocular tubular pore, end and side, × 1,500

pairs, much smaller, but large, simple, with somewhat bell-shaped atrium, situated, in early undistended adult females, well up on the dorsal surface; derm pores numerous and varying conspicuously in size, number of loculi, chitinization, and relative abundance of different sorts, the quadrilocular disk type, with variations and modifications, usually making up the dense band of pores surrounding the marsupial opening, genital opening surrounded by a cluster of

large, lightly chitinized multilocular disk pores, other more or less heavily chitinized multilocular pores scattered over both surfaces; the large bilocular tubular marginal ducts of the larva represented by small clusters of similar disk pores along the body margin; derm spines present, numerous over both dorsal and ventral areas, one sort extending almost to the marsupial opening, to the thoracic spiracles, and to the coxal insertions ventrally, another, or the same sort slightly modified, occurring between the legs, these spines varying with the species in general appearance, accompanied by dense marginal clusters of elongate cylindrical spines swollen at bases and slightly clavate at apices, these clusters evidently the foundation for the marginal secretionary wax tufts; body hairs, as understood here, occurring ventrally, not very numerous, most abundant within and around the marsupial opening, of the usual slender shape with expanded bases; derm setae more abundant than hairs, present on both surfaces, the basal collars varying from flat to high cylindrical, a scattered

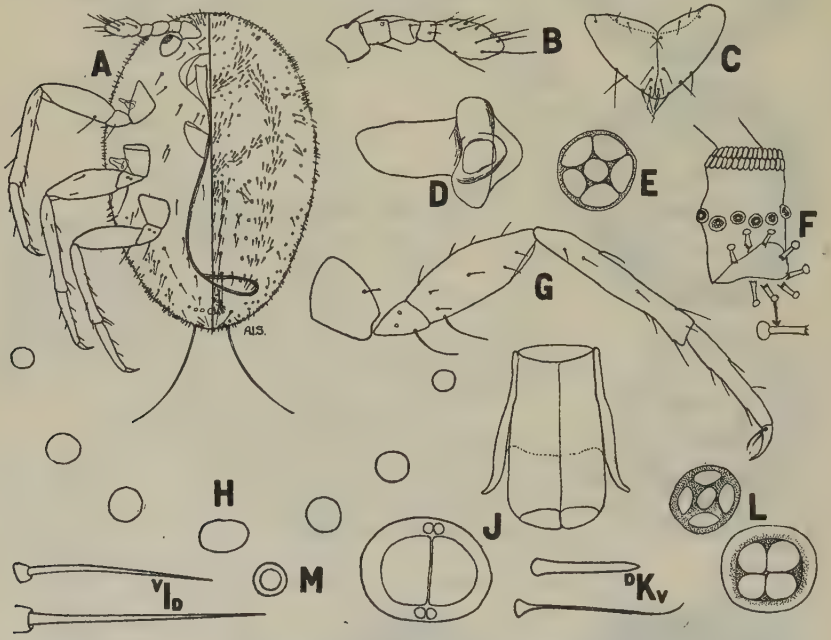

FIG. 77.—*Aspidoproctus mirabilis*, larva: A, outline, dorsal and ventral, × 60; B, antenna, × 115; C, beak, × 115; D, thoracic spiracle, × 460; E, ventral derm pore, × 1,500; F, anal tube, × 330, with detail of seta, × 650; G, leg, × 115; H, ventral cicatrices, × 330; I, derm setae, ventral (V) and dorsal (D), × 650; J, large marginal tubular pore, surface and section, × 1,500; K, derm spine (D) and ventral hair (V), × 650; L, dorsal derm pores, × 1,500; M, abdominal spiracle, × 1,500

cluster around anal opening larger, those along body margin not conspicuously large, those occurring dorsally usually stouter and somewhat shorter than the ventral ones; anal tube short, lightly chitinized except inner end, this heavily chitinized and with ring of wax pores and a ring of tiny tubercles at apex of invagination of inner end; ventral cicatrices very abundant, apparently scattered, but in two wide bands, extending on each side of ventral and marginal areas from antennae to a meeting point behind marsupial opening, each band made up of transverse irregular rows of cicatrices, these varying extensively in size and in number to the row.

Intermediate female.—In general similar to the early adult female in morphological characters, at least; marsupial structures lacking.

Larva.—Approximately elliptical in outline; derm membranous; antennae short and stout, five-segmented, the terminal segment largest, distinctly swollen, but not clavate, each segment with a few small setae, those on the apical larger and including a few stout sensory setae, none of the setae long as in iceryine

genera; legs rather long and slender, the trochanter with two pairs of sensory pores, the claw with usually three fairly distinct denticles within, the claw digitules slightly exceeding apex of claw, very slender in apical portions; beak very short and stout conical, one-segmented, the apical sensory setae acute or bluntly rounded at tips, in no case broadened or divaricate; thoracic spiracles large, with bar; abdominal spiracles in seven pairs, minute, simple; derm pores including, along the margin, enlarged bilocular tubular pores producing glassy threads, ventrally a few quadrilocular disk and a few with, usually, six loculi and triangular center, at margin and dorsally with longitudinal rows of larger quadrilocular disk pores and pores with triangular center and six loculi, those in anal tube collar and scattered ring around anal opening with oval center and more numerous loculi (nine or more); body spines numerous and relatively large, asymmetrical in shape, stout, tapering, those in median dorsal row sometimes symmetrical and nearly cylindrical but with pointed tips, these spines arranged in five longitudinal rows dorsally, a median, two intermediate, and two marginal; a few inconspicuous hairs, slender with strongly expanded bases; setae not numerous, small and inconspicuous, except a few in the posterior section of the median spine band and a single pair of long apical setae, no other marginal setae enlarged; anal tube not chitinized except around the collar of polygonal wax pores at inner end, with a circle of almost contiguous multilocular disk pores within the opening, a circle of curious short setae with flattened, fringed tips around the opening, and outside of these a circle of widely separated multilocular disk pores; ventral cicatrices in a transverse curved row beneath the anal tube, seven in number (in the species examined), the median largest, all approximately circular in shape.

Adult male.—Of the usual elongate shape, anterior apex of head triangular; antennae stout, the segments beyond the second distinctly trinodose and each with three whorls of long setae, the apical and preapical segments approximately equal in length; wings of the usual shape, venation, and dark color, the apex of the diagonal vein tending to approach the margin somewhat as in Drosicha, rather than stopping short as in Icerya; legs rather stout for males of this subfamily, the anterior femur with a considerable number of bifurcate setae, claw rather stout, claw digitules not attaining claw apex; abdomen more chitinized and without the definitely formed dorsal pattern of Drosicha; derm bearing numerous relatively long, slender setae and normally quadrilocular disk pores in transverse rows; abdominal spiracles probably in seven pairs, relatively inconspicuous, simple; with a single apical pair of elongate fleshy tassels, lateral margins of some segments anterior to apical more or less protuberant and bearing clusters of longer setae; penis sheath stout, tapering nearly uniformly but not so very strongly from base to apex, this last bluntly rounded and bearing numerous sensory pores.

As at present recognized, the genus is wholly African in its distribution, and chiefly subequatorial, although the three subregions, East African, West African, and South African, of the Ethiopian region have representatives that have been assigned here.

As with most other genera, the information concerning the biology of the included species is more or less fragmentary. The published statements of Lounsbury (*117*) and Brain (*3, p. 179*) (on the basis of information furnished by R. W. Jack) show that there is one generation annually, with egg production and larval hatching in spring (Southern Hemisphere), larval growth throughout the summer, male emergence in the fall with fertilization of the female at this time, and slow female growth till early spring, when full maturity and complete development of the ovaries are rapidly attained.

Although the generic diagnosis given above has been drawn up on the basis of two species only, *maximus* and *mirabilis*, and only these two can, in consequence, be regarded as certainly included in the genus as here defined, the unit is so characteristic that it seems practically certain that all of the 18 species that have been assigned to the genus (including Lophococcus) actually may be properly included in it.

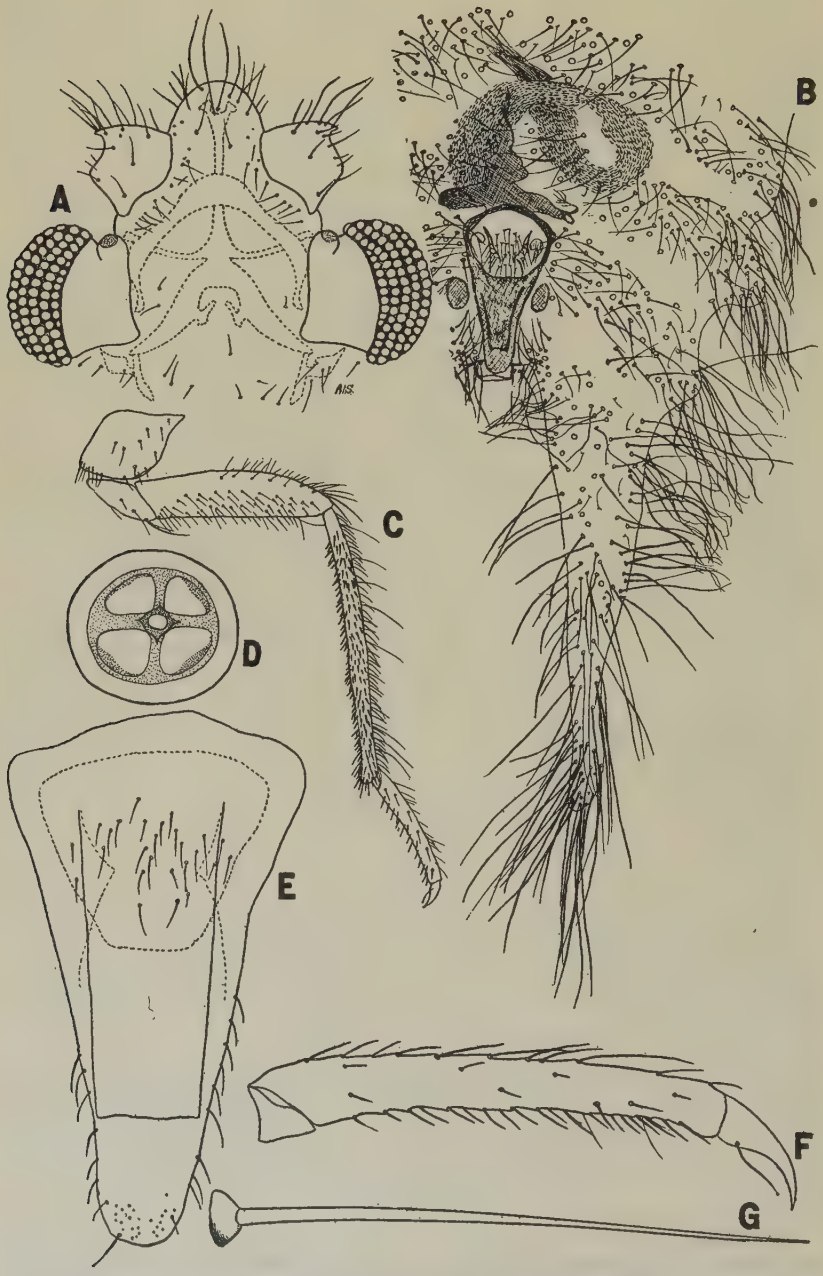

FIG. 78.—*Aspidoproctus maximus* (except E), adult male: A, head, × 50; B, apex of abdomen, × 42.5; C, leg, × 30; D, derm disk pore, × 1,500; E, *A. mirabilis*, penis sheath, ventral, × 120; F, tarsus and claw, × 120; G, abdominal seta, × 650

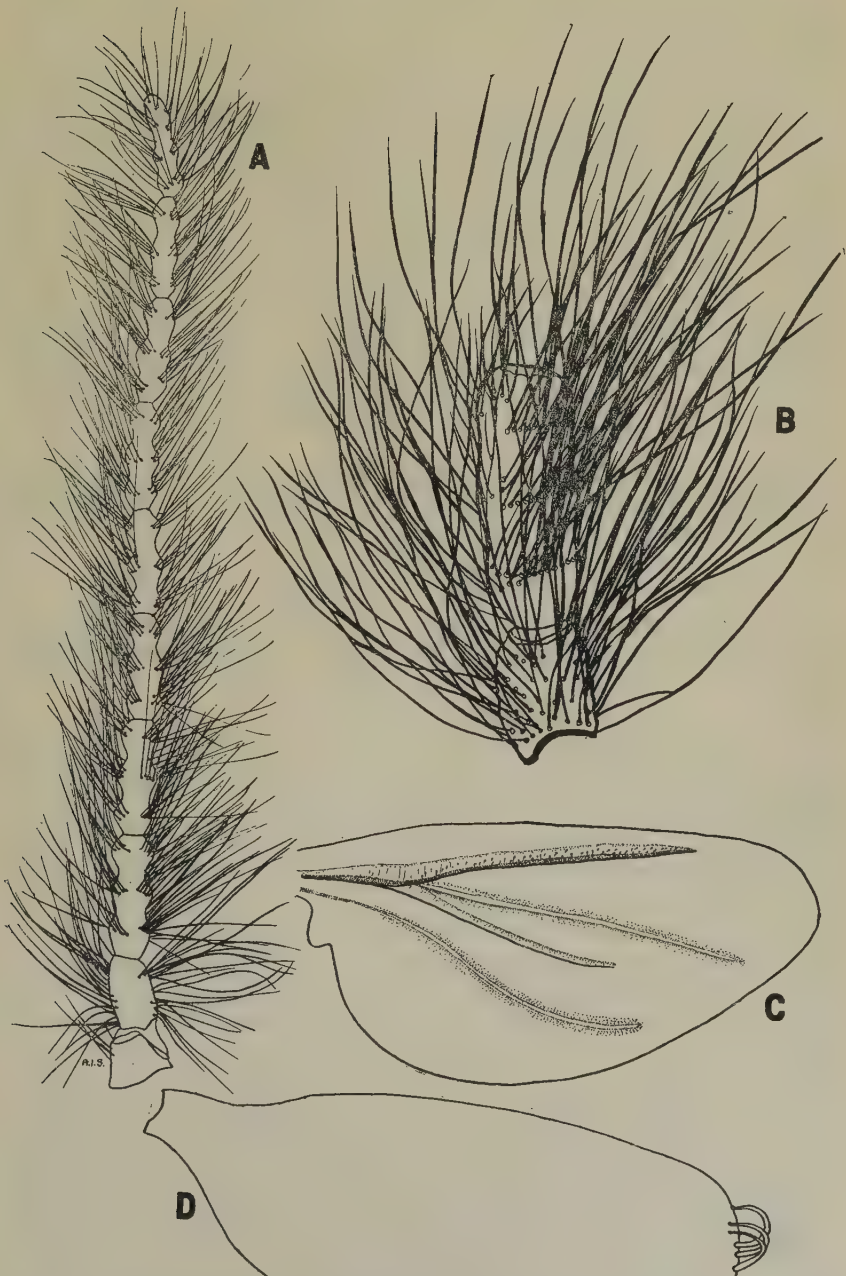

FIG. 79.—*Aspidoproctus maximus* (except C), adult male: A, antenna, × 30; B, second and third antennal segments, × 60; C, *A. mirabilis*, wing, × 12; D, halter, × 120

The complete list of these species includes *armatus* Newstead (*148, p. 157*), from Tanganyika Territory and Rhodesia; *bouvieri* Vayssière (*166, p. 333*), from French Equatorial Africa; *carinatus* Lindinger (*114, p. 87*), from Tanganyika Territory; *cassiae* Laing (*170, p. 280*) (nom. nud.), *congolensis* Vayssière (*170, p. 285*), from Belgian Congo; *ellenbergeri* Vayssière (*170, p. 285*), from Upper Zambesi; *ghesquierei* Vayssière (*170, p. 288*), from Belgian Congo; *giganteus* Newstead (*150, p. 303*), from Nigeria; *glaber* Lindinger (*114, p. 87*), from Tanganyika Territory; *gowdeyi* Newstead (*152, p. 177*),[27] from Uganda; *maximus* Lounsbury (*117, p. 32*), from Tanganyika Territory and Rhodesia; *mimeuri* Vayssière (*169, p. 31*), from French West Africa; *mirabilis* Cockerell (*21, v. 34, p. 227*), from Natal, Transvaal, and Cape Province; *neavei* Newstead (*151, p. 4*), from Nyassaland; *parvus* Lindinger (*114, p. 89*), from Tanganyika Territory; *pertinax* Newstead (*143, p. 947*), from Nyassaland and Rhodesia; *tricornis* Newstead (*149, p. 17*), from Southwest Africa and Transvaal, *verrucosus* Newstead (*151, p. 5*), from Uganda; and *vuilleti* Vayssière (*165, p. 424*), from French West Africa.

In the absence of specimens of the great majority of these species, no effort has been made even to form an opinion as to the probable validity of each of the whole list given.

TRIBE DROSICHINI MORRISON

The writer (*136, p. 105*) has just erected this tribe for the reception of the genus Drosicha Walker and two other closely related genera.

Tribal Characteristics

Habit.—Living exposed on the trunk, branches, and twigs of the host; at oviposition seeking concealment at the base of the host tree and depositing the eggs in a mass of cottony secretion forming a loose ovisac.

Adult female.—Body elliptical in outline, length range extensive (6 to 18 mm. or more); derm at full maturity remaining membranous or becoming fairly heavily chitinized and yellow brown; antennae normally eight-segmented or nine-segmented, tapering gradually, the apical segment longest, the sensory setae not sharply differentiated; legs stout, the trochanter mostly with two pairs of sensory pores, the setae on under sides of tibia, tarsus, and frequently of femur quite stout, spinelike, claw stout, digitules hardly attaining tip of claw; beak fairly long conical, three-segmented, the basal a narrow collar, joint between second and third sometimes rather obscure, apical sensory setae numerous, acute at tips; thoracic spiracles large and stout, with bar and with or without definite cluster of disk pores at opening; abdominal spiracles much smaller, but large as compared with some other tribes, in seven pairs, with or without a collar of disk pores within opening; derm pores relatively simple, not heavily chitinized, with three, four, five, or six loculi, some, a different sort, around or near spiracles and anal opening, with 9 to 11 loculi; no spines present on derm; setae present, relatively few and small dorsally and ventrally, much larger and more conspicuous along body margin, here occurring singly or in clusters; derm hairs very abundant over both surfaces, larger ventrally and along margin, usually slender and quite hairlike, sometimes stouter, approaching a spinelike form; anal tube short, relatively heavily chitinized, the inner end with chitinized extension often U-shaped or V-shaped, and usually with a single row of polygonal wax pores, these sometimes wanting or completely obscured; with three large, oval, closely approximated ventral cicatrices.

[27] According to Vayssière (*170, p. 309*), who examined specimens, this species should be assigned to the genus Steatococcus.

Intermediate stage female.—So far as known, in general resembling the adult female.

Larva.—Elliptical in outline, relatively large in size; derm membranous; antennae five-segmented, the third and fifth segments long, the sensory setae not definitely differentiated; legs fairly stout, the setae slender, claw without definite denticles, although often roughened within near tip, digitules not exceeding apex of claw; beak fairly distinctly three-segmented, the basal a narrow collar, the apical sensory setae numerous, acute at apices; thoracic spiracles large, with bar and single disk pore at opening; abdominal spiracles much smaller, simple, each with enlarged chamber and disk pore immediately adjacent; derm pores scattered, relatively simple, not heavily chitinized, those over most of body usually with six loculi, those next to spiracles and around anal opening with more, usually with nine loculi; derm setae not very abundant, fairly large, but varying considerably in length with the species, those along margin larger, the arrangement varying from only the apical pair greatly elongated to a complete marginal series of very long setae; no derm spines developed; derm hairs abundant, particularly dorsally, here in broad, transverse, hardly differentiated bands, individual hairs small and slender; anal tube short, fairly heavily chitinized, and with chitinized prolongation or widening of inner end, without polygonal wax pores; with a single, large, median, circular to oval, ventral cicatrix.

Adult male.—Of the usual elongate shape; size varying considerably with the species; apex of head triangular in outline; antennae long, usually equaling or exceeding body in length, all segments beyond second trinodose and with three whorls of long setae, this condition often obscured in the terminal segment, this last varying with the species from as long as to more than twice as long as the preapical; wing of the usual shape, but more elongate and tapering more apically than is characteristic for the Iceryini, with costal margin bright red or, more frequently, quite dark as is the remainder of the wing, with the basal diagonal vein almost attaining the wing margin, and with two conspicuous diagonal clear lines; halteres large, flattened, with about five large, curved, knobbed setae at apex of each; legs slender but stouter than in many other groups, the trochanter with two or more sensory pores on each face, the tibia and tarsus with many bifurcate setae, the anterior femur with a few to many such setae, claws without denticles, claw digitules approximating the apex of the claw; abdomen with membranous derm, except for an irregular chitinized pattern dorsally; margin of abdominal segments with two to six pairs of fleshy tassels; penis sheath more or less triangular in outline, either with sides nearly straight or more or less conspicuously constricted, with the apical section becoming narrow and cylindrical, bearing sensory pores at apex and small setae along margin; fleshy penis bearing many hairs or slender spines and, in a patch near inner end, small fimbriate plates; abdominal spiracles in seven pairs, tubular, opening a circular collar or elongate irregular slit; only the single, normally quadrilocular, rarely trilocular or pentalocular type of disk pore present; derm of body bearing slender setae only, those on abdomen in transverse bands, often abundant and rather long.

The known distribution of the species definitely included here comprises the Manchurian subregion of the Palaearctic region, and the Indian, Indo-Chinese, and Indo-Malayan subregions of the Oriental region.

Between the extended and careful work of Kuwana (*107*, *p. 19*, *37*, *47*) in Japan and notes on various Indian species, for example, those by Stebbing (*161*, *p. 144*) and Maxwell-Lefroy (*129*, *p. 111*), there is, compared with the knowledge of some other groups, a large amount of information available regarding the biology of these species. So far as generalizations may be drawn from the specific details published, the members of the tribe have one generation annually and are oviparous, with oviposition usually taking place in the loose soil or in rubbish at the base of the host tree. The life history possesses an apparently peculiar twist in that the egg stage is very greatly extended, but through the hotter months of the year, and in that the active growing season occurs during the winter and early

spring months of the year. Thus, in general, the eggs hatch in November or December, the adult female reaches maturity from late April to early June, with oviposition following shortly thereafter, and the remaining period of the summer and fall months is passed in the egg stage.

It has been found necessary to add to the long established genus Drosicha Walker two new genera, based respectively on adult female and on adult male stage only of previously described species, in order to accommodate properly all of the species believed to be definitely assignable to this tribe.

These genera may be separated by the following keys:

KEYS TO GENERA OF DROSICHINI

ADULT FEMALE

a. Abdominal spiracles simple, that is, without a pore collar_____Drosicha
aa. Abdominal spiracles each with a conspicuous pore collar_____Drosichiella

The adult female of the genus Drosichoides is unknown.

ADULT MALE

a. Penis sheath strongly tapering, the apex produced into a slender, almost cylindrical style with rounded tip; apical antennal segment, while usually longer than preapical, not more than one and a half times as long as that segment_____Drosicha
aa. Penis sheath much stouter, tapering gradually to apex, not constricted; apical antennal segment conspicuously elongated, more than twice length of preapical _____Drosichoides

The adult male of Drosichiella is not certainly known.

GENUS DROSICHIELLA MORRISON

(Pl. 5, E, and figs. 80 and 81)

This genus was recently established by the writer (*136, p. 105*) for the reception of two described species that were originally assigned to the genus Monophlebus. One of these, *Monophlebus tamarindus* Green, has been selected as the genotype.

GENERIC CHARACTERISTICS

Habit.—Presumably identical with that given for the tribe.

Adult female.—Closely resembling Drosicha in most characteristics; size medium to fairly large (8 to 14 mm. long); body elliptical; derm becoming quite definitely chitinized and yellow brown at maturity, with large circular to oval areoles around the pores and the seta and hair bases; antennae eight-segmented, stout, the terminal longest, the sensory setae not conspicuously differentiated; legs stout, the trochanter with two pairs of sensory pores, the setae on the under side of femur, tibia, and tarsus quite stout to spine-like, claw stout, length of digitules uncertain; beak conical, fairly distinctly three-segmented, the basal narrow, apex with about 16 sensory setae; thoracic spiracles large, with a cluster or band of disk pores at opening, abdominal spiracles in seven pairs, likewise relatively large, with a complete band of disk pores (numbering from 11 to 30 in specimens examined) within the atrium of each; derm pores relatively simple, not conspicuously developed or chitinized, numerous but less abundant than the hairs, appearance varying somewhat, number of loculi varying from 3 (rare) to as many as 11, 4, 5, and 6 occurring most frequently, the dorsal pores, in general, with fewer loculi than the ventral, those pores associated with the spiracles with the greatest number of loculi; derm setae few, not large in median areas,

although larger than hairs, much larger along margin, the marginal clusters found in Drosicha represented only by isolated large setae; body hairs numerous, varying in size individually and with the species, the dorsal averaging

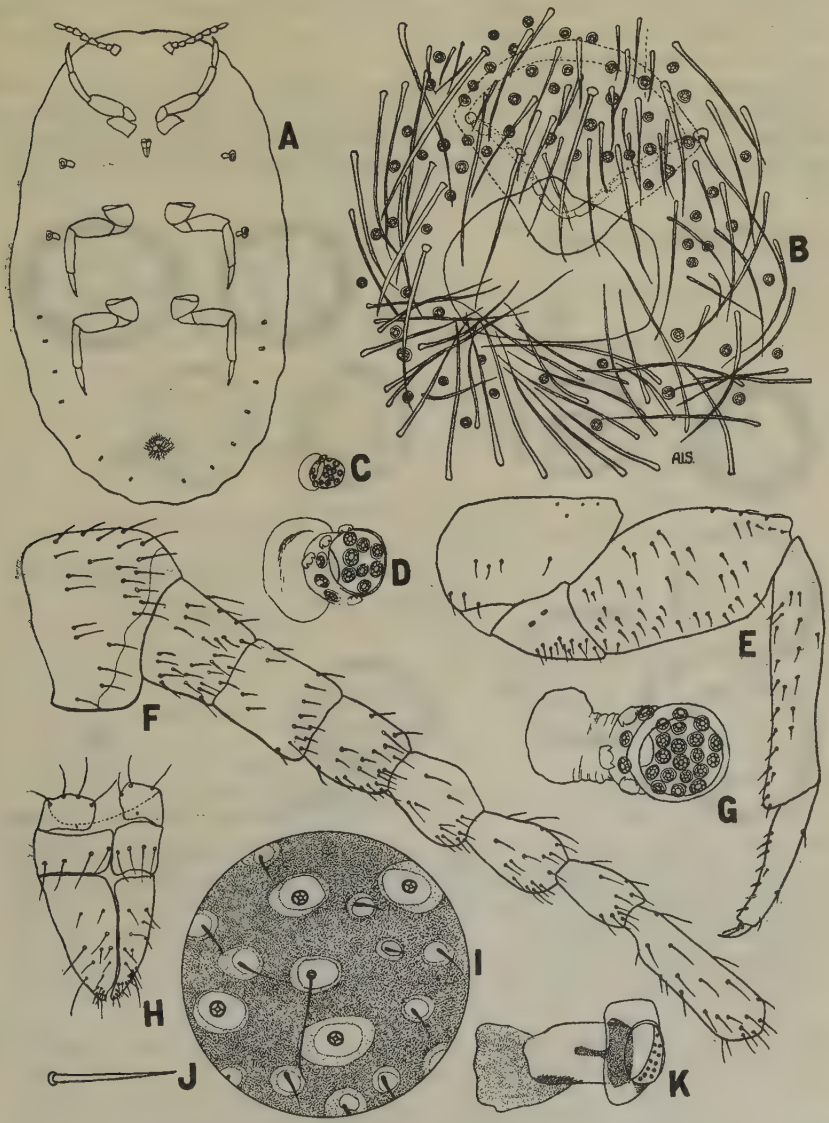

FIG. 80.—*Drosichiella* spp., adult females: A, *tectonae* outline, optical section, × about 5; B, *tectonae*, anal region, × 165; C, *tamarinda*, abdominal spiracle, × 120; D, the same, × 230; E, *tamarinda*, leg, × 30; F, *tamarinda*, antenna, × 60; G, *tectonae*, abdominal spiracle, × 230; H, *tamarinda*, beak, × 60; I, *tamarinda*, section of dorsal derm showing chitinization, × 60; J, *tamarinda*, sensory seta from beak apex, × 230; K, *tamarinda*, thoracic spiracle, × 60

distinctly shorter than the ventral, all resembling those of Drosicha, although somewhat stouter and less attenuated toward apices; anal tube short, chitinized, with circular or distorted inner end, and this more heavily chitinized

and bearing a ring of wax pores; with three large, closely associated ventral cicatrices as in Drosicha.

No other stages are known; some one of the males that have been described, without association with females, from India or Ceylon may possibly represent a male of this genus, but no evidence showing this has been produced.

Two species included here, *phyllanthi* (Green) (*75, p. 169*) from Ceylon and *tamarinda* (Green) (*66, p. 17*) from India, have been associated together by Green (*78, p. 338*) on the basis of the presence of disk pores within the atrium of each abdominal spiracle, while the

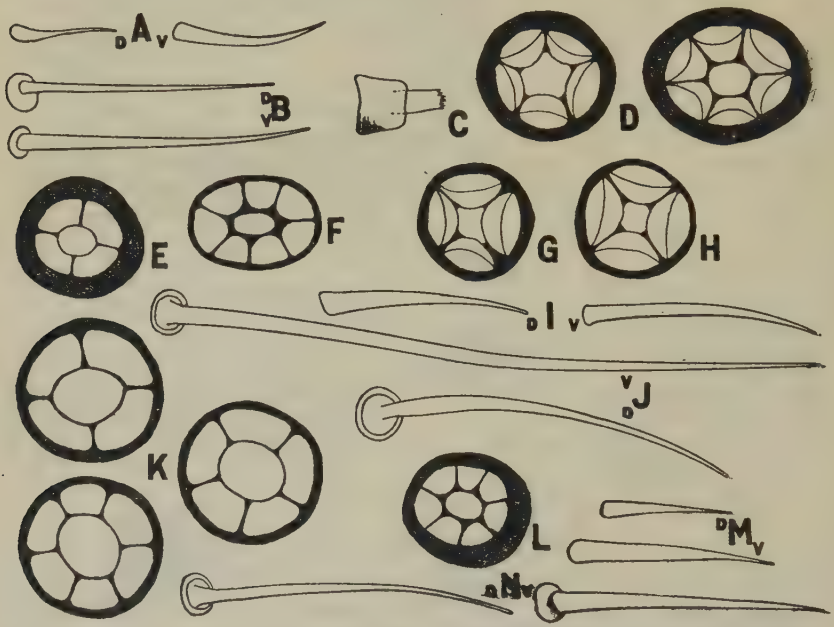

FIG. 81.—*Drosichiella* spp., adult females: A, *tamarinda,* hairs, dorsal (D) and ventral (V), × 600; B, *tamarinda,* setae, dorsal (D) and ventral (V), × 600; C, *tamarinda,* base of largest type marginal seta, × 650; D, *phyllanthi,* dorsal (left) and ventral (right) derm pores, × 1,500; E, *tamarinda,* dorsal derm pore, × 1,500; F, *tamarinda,* spiracular pore, × 1,500; G, *phyllanthi,* dorsal derm pore, × 1,500; H, *phyllanthi,* ventral derm pore, × 1,500; I, *phyllanthi,* derm hairs, dorsal (D) and ventral (V), × 600; J, *phyllanthi,* setae, dorsal (D) and ventral (V), × 600; K, *tamarinda,* ventral derm pores, × 1,500; L, *tectonae,* derm pore near anal opening, × 1,500; M, *tectonae,* hairs, dorsal (D) and ventral (V), × 600; N, *tectonae,* setae, dorsal and ventral, × 600

third is based on specimens that appear to have been regarded previously as representing one of these species.

KEY TO SPECIES OF DROSICHIELLA

a. The great majority of the dorsal disk pores with more than four loculi; body hairs quite long, middorsal about 72 μ, midventral about 98 μ, ratio 1 to 1.35 ..... *phyllanthi* (Green)

aa. The great majority of the dorsal disk pores quadrilocular; body hairs shorter, middorsal hardly more than 35 μ, midventral hardly more than 55 μ.

b. About 25 to 30 multilocular disk pores within the atrium of each abdominal spiracle; middorsal hairs about 35 μ, midventral hairs about 55 μ, ratio 1 to 1.6 ..... *tectonae* Morrison

bb. About 12 to 18 multilocular disk pores within the atrium of each abdominal spiracle; middorsal hairs about 24 μ, midventral hairs about 50 μ, ratio 1 to 2 ..... *tamarinda* (Green)

Genus Drosicha Walker

(Pls. 5, F, and 6, A, and figs. 82, 83, 84, 85, and 86)

This genus was established by Walker (*171, p. 306*) in 1858, at which time only a single species, *contrahens* Walker, was included. The original specimen of this species has recently been redescribed by Green (*75, p. 168*) in sufficient detail to demonstrate clearly its nature and its relationships. From this description and from a study of a considerable series of species from eastern and southeastern Asia and adjacent areas it is evident that the genus forms a legitimate natural group at present known to occur only in these regions.

Some synonyms of Drosicha have been erected. These include Cockerellella MacGillivray (*119, p. 71*), established with the *Monophlebulus townsendi* of Cockerell as type; Greeniella MacGillivray (*119, p. 70*), subsequently replaced by Greenacoccus MacGillivray (*119, p. 474*), with *Monophlebus stebbingii* Stebbing as type; and Warajicoccus Kuwana (*107, p. 7*) with *M. corpulentus* Kuwana as the type.

GENERIC CHARACTERISTICS

Habit.—As given for the tribe.

Adult female.—Body more or less covered by secretion, but this not concealing it, elliptical in outline, length varying greatly, range from as little as 7 to as much as 19 mm.; derm remaining membranous or becoming somewhat chitinized and yellowish at maturity; antennae normally eight-segmented to nine-segmented, stout, terminal segment elongated, each segment bearing numerous fairly stout setae, the sensory type not definitely differentiated; legs stout, the lower faces of tibia and tarsus and, to some extent, of the femur, bearing stout, spinelike setae, claw stout, curved, no definite denticles, but inner face often roughened, claw digitules stout at base, tapering to slender acute tips, not attaining apex of claw; beak rather elongate conical, appearing fairly distinctly three-segmented, the sensory setae at apex tapering to blunted points; thoracic spiracles large, with bar and a few pores near mouth; abdominal spiracles in seven pairs, placed within the margin dorsally, simple, each a short cylindrical tube at the opening with a more or less expanded inner end; derm pores of one simple disk type only, with from five to seven loculi, fairly abundant but not crowded both dorsally and ventrally, in general larger ventrally, particularly in the genital region, and some here with more loculi; derm without spines; with setae of moderate size over the surface, these becoming relatively very large and conspicuous along body margin; usually with very numerous, almost always curved, hairs distributed nearly uniformly over the body, sometimes, according to the species, more or less abundant and larger or smaller dorsally than ventrally; anal opening simple, surrounded by a dense cluster of hairs and setae, anal tube short, heavily chitinized at the inner end, the chitinized portion usually taking the form of a U-shaped or V-shaped yoke open anteriorly or closed by cross chitinization, a single, sometimes incomplete row of polygonal wax pores probably retained in all species, but often completely obscured by the heavy chitinization; with three large, oval, ventral cicatrices placed close together behind genital opening, often more or less completely obscured by a dermal invagination at the point of occurrence.

Larva.—Of relatively large size, up to nearly half a millimeter, elliptical; derm membranous; antennae five-segmented, the third and last longer, antennal setae varying from short to long; legs stout, the setae long and slender, claw with one or more denticles, claw digitules short at base, tapering; apices more or less distinctly knobbed, approaching the claw apex; beak long or short conical, more or less obviously three-segmented, basal collar narrow, apical sensory setae acute or rounded at tips; thoracic spiracles with bar and usually with one pore at opening; abdominal spiracles much smaller, tubular, the open-

ing of each with a disk pore immediately adjacent; derm disk pores of two sorts, one usually with six loculi, these scattered over the dorsal surface and the margin of the ventral surface, the other with from 8 to 11 loculi distributed

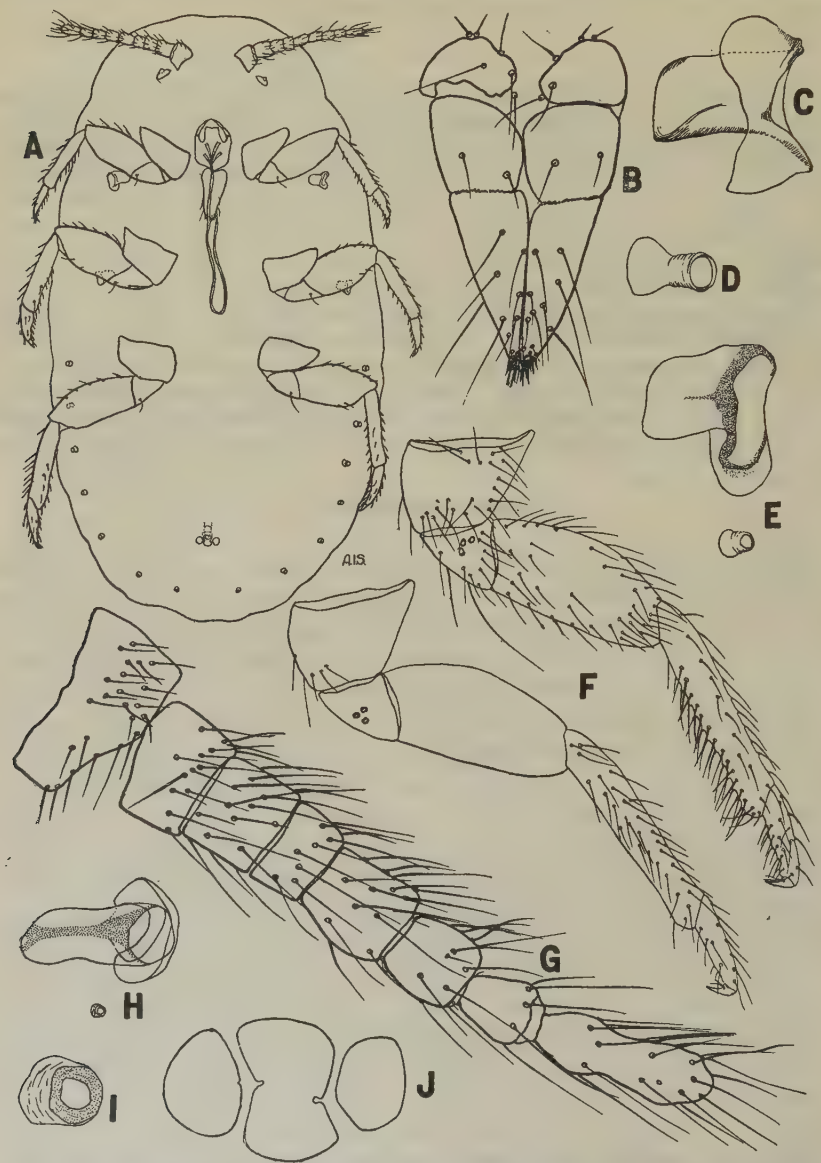

FIG. 82.—*Drosicha* spp., adult females: A, *corpulenta,* outline, optical section, × 7.5; B, *corpulenta,* beak, × 60; C, *stebbingii,* thoracic spiracle, × 60; D, *stebbingii,* abdominal spiracle, × 120; E, *corpulenta,* thoracic and abdominal spiracles, × 115; F, *maskelli,* legs, opposite faces, × 26.5; G, *?contrahens,* antenna, × 60; H, *maskelli,* thoracic and abdominal spiracles, × 57.5; I, *maskelli,* abdominal spiracle, × 335; J, *corpulenta,* ventral cicatrices, × 60

over the remainder of the venter and around the anal opening dorsally; body with numerous hairs in transverse rows ventrally, and with large marginal setae, typically in pairs, one larger, one smaller, at the margin of each seg-

ment on which they occur, but the number of large marginal setae developed ranging from the two apical pairs to a complete series, and the lengths ranging from about two-fifths the body length to more than one and a half times the body length; anal tube very short, chitinized, inner end in some species suggesting the U-shape of the adult, in others cylindrical, with a ring of disk pores outside the opening proper but no wax pores retained at the inner end; with a single, large, circular to oval, ventral cicatrix.

Adult male.—Of the usual elongate shape, naked or with scanty grayish secretion on abdomen and prothorax; apex of head triangular in outline; antennal segments beyond the second each with three distinct whorls of setae and usually distinctly trinodose, this condition sometimes slightly obscured on the third segment and often much confused on the apical segment, this last slightly longer

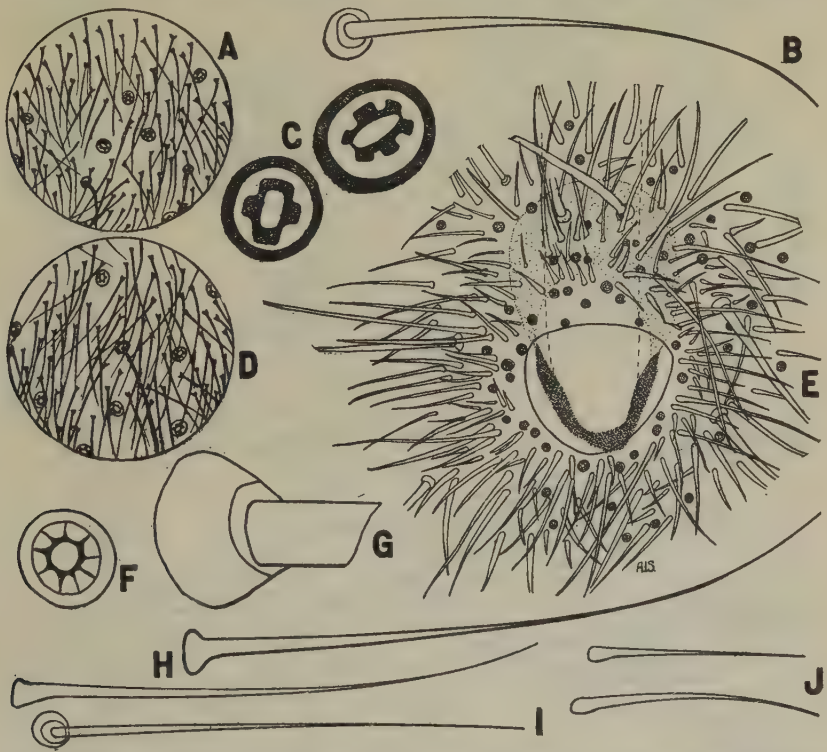

FIG. 83.—*Drosicha* spp., adult females: A, *maskelli*, section of midventral derm, × 220; B, *?contrahens*, middorsal seta, × 650; C, *maskelli*, derm pores, × 1,500; D, *maskelli*, section of middorsal derm, × 220; E, *corpulenta*, anal region, × 120; F, *?contrahens*, disk pore near anal opening, × 1,280; G, *?contrahens*, base of largest type marginal seta, × 650; H, *?contrahens*, midventral hairs, × 650; I, *?contrahens*, midventral seta, × 650; J, *?contrahens*, middorsal hairs, × 650

than to half again as long as preapical; wing of the usual shape, quite dark in color, with a somewhat lighter costal border, with basal diagonal only developed, its apex closely approaching the wing margin and with the usual diagonal clear lines; halteres flattened, with several curved and knobbed apical setae; legs slender, but more substantial than in many other genera, the anterior femur always with a few to many bifurcate setae, claw slender, claw digitules very delicate at tips, hardly attaining claw apex; derm of abdomen membranous, but bearing dorsally a more or less distinctly marked pattern formed by irregular slightly chitinized and darkened areas, margins of abdominal segments, numbering from the apical, bearing from two to six pairs, more or less fully developed, of long, fleshy tassels; penis sheath characteristic in shape, broad at base, strongly tapering, the apical portion forming an almost parallel-sided protuberance terminating in a rounded tip bearing sensory pores; ab-

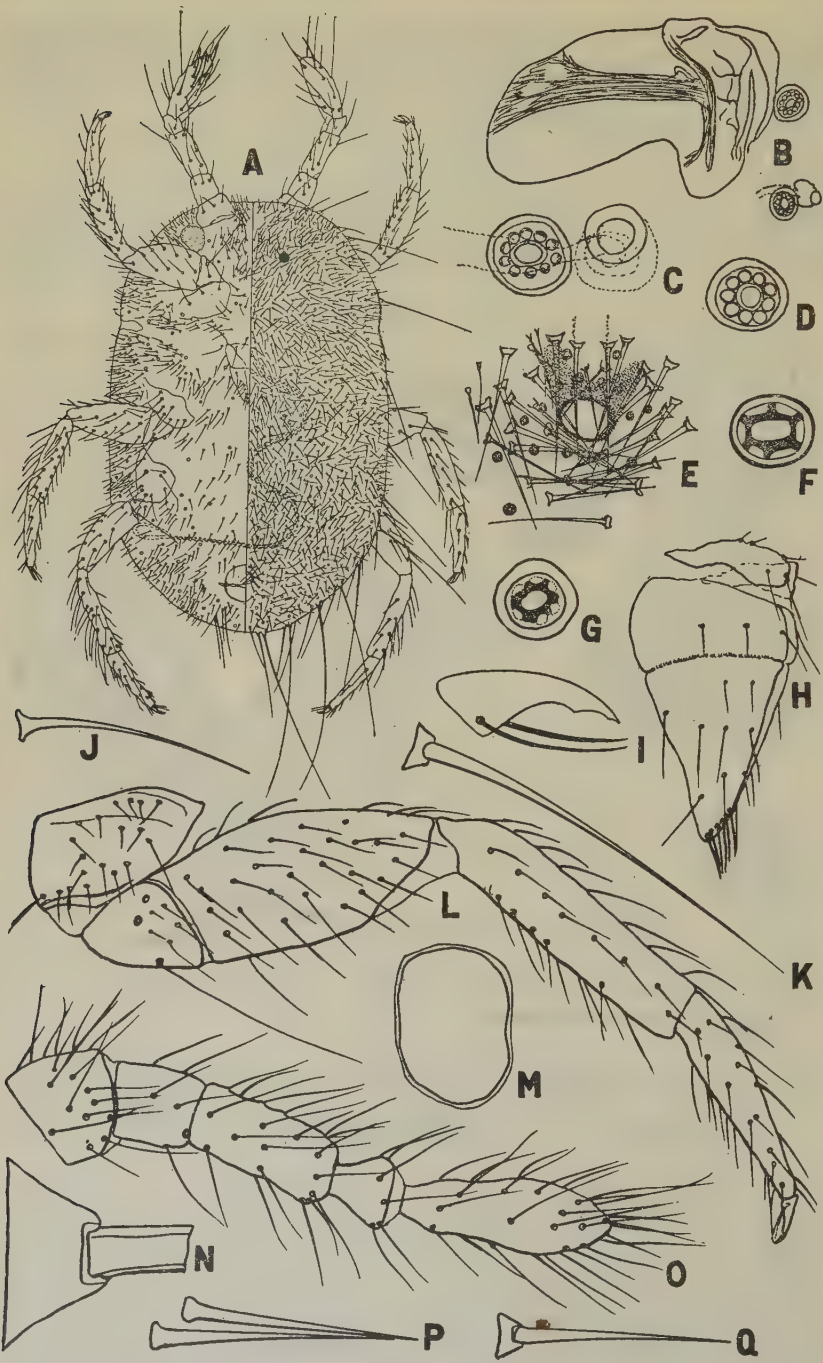

FIG. 84.—*Drosicha corpulenta* (except A, F, I, these *D. maskelli*), larva: A, outline, dorsal and ventral, × 57.5; B, thoracic spiracle and abdominal spiracle, × 650; C, abdominal spiracle and adjacent disk pore, × 1,280; D, disk pore near thoracic spiracle and near anal opening, × 1,280; E, anal area, × 330; F, dorsal derm pore, × 1,500; G, dorsal and ventral derm pore, × 1,280; H, beak, × 115; I, claw, × 640; J, ventral hair, × 650; K, ventral seta, × 650; L, leg, × 115; M, ventral cicatrix, × 165; N, base of largest type marginal seta, × 650; O, antenna, × 115; P, dorsal hairs, × 650; Q, dorsal seta, × 650

dominal spiracles simple, short tubular, mostly well developed and obvious, in seven pairs; only a single pore type present, this quadrilocular disk; head and apex of abdomen, sometimes at least, bearing tiny tubercles, remainder of body with slender setae only, these varying much in size.

The species that have been included in this genus, on the basis of the material available for study, appear to fall more or less naturally into two groups, chiefly through their geographical distribution. Unfortunately, these groups, again on the basis of the available study material, do not offer any very clear-cut, tangible key characters by which they may be definitely separated on morphological grounds.

No larvae from any of the Indian species have been available for examination, and the larval segregation is therefore uncertain.

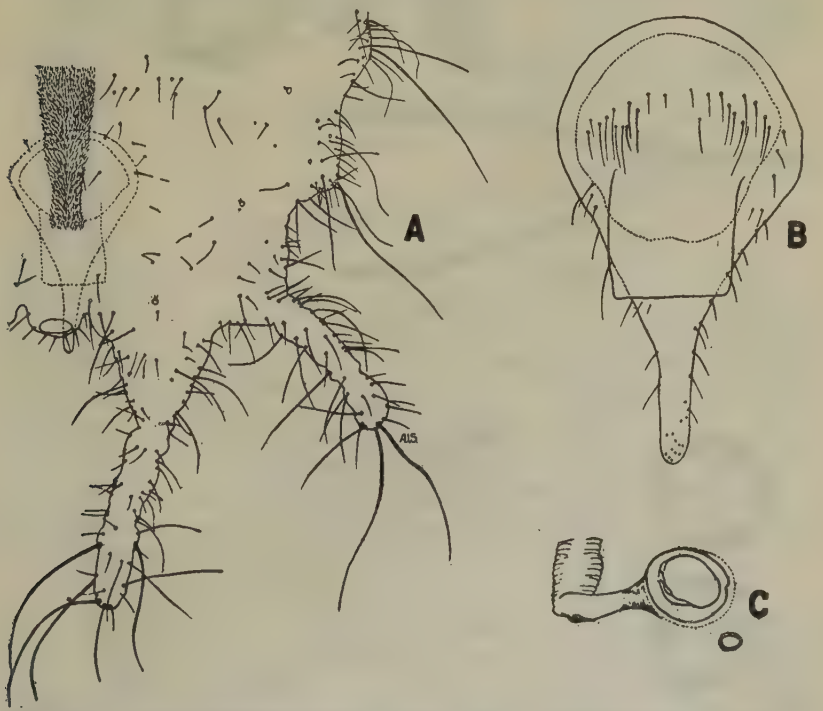

FIG. 85.—*Drosicha contrahens*, adult male: A, apex of abdomen, dorsal, × 60; B, penis sheath, ventral, × 120; C, abdominal spiracle, × 1,500

GROUP 1. SPECIES OF THE PALAEARCTIC REGION, MANCHURIAN SUBREGION

The species included here are *contrahens* (Walker) (*171, p. 306*), *corpulenta* (Kuwana) (*102, p. 46*), *howardi* (Kuwana) (*107, p. 40*), and *pinicola* (Kuwana) (*107, p. 29*). The adult females, and indeed all stages of these species, are extremely difficult to separate, and precise key characters for such separation have not as yet been discovered. The very detailed and elaborately illustrated work by Kuwana (*107*) on the three Japanese species is so full that no attempt is made here to add to its treatment. No specimens certainly identical with *contrahens* (Walker) have been examined, although specimens received from Peking, China, and agreeing very well with Green's (*75, p. 168*) redescription of this species have been studied. These

are evidently closely related to *D. corpulenta* (Kuwana). Unfortunately no larvae of this Chinese species are available; this stage might supply a key indicating the closeness of this relationship.

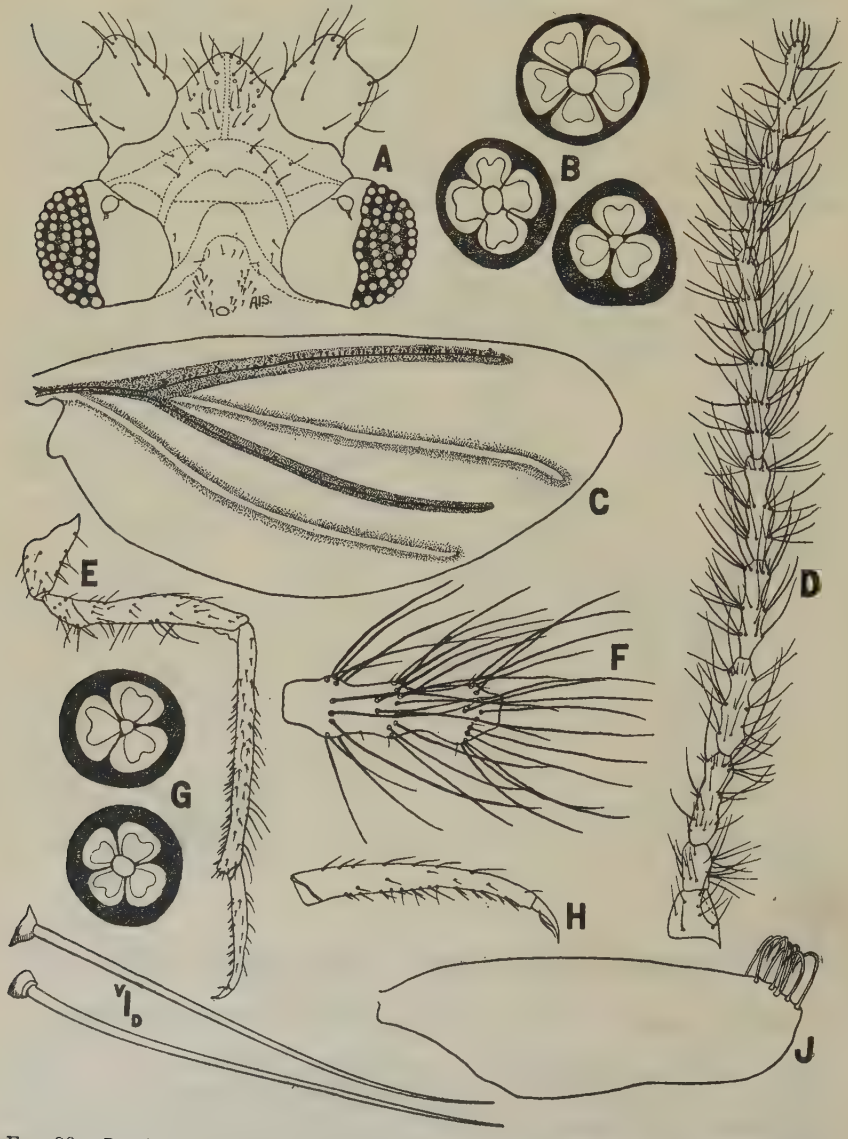

FIG. 86.—*Drosicha contrahens*, adult male: A, head, dorsal, × 60; B, derm pores, dorsal, × 1,500; C, wing, × 17.5; D, antenna, × 30; E, leg, × 30; F, third antennal segment, × 50; G, derm pores, ventral, × 1,500; H, tarsus and claw, × 60; I, abdominal setae, ventral (V) and dorsal (D), × 650; J, halter, × 120

At present the only structural characters that appear to offer much definite prospect of utility in separating the adult females are found in the actual and relative lengths of the hairs which clothe the bodies of these insects. Even here, the precise utility is somewhat doubtful.

The males belonging to these species are likewise very close and difficult to separate. A tentative key for distinguishing them is offered below.

Key to Drosicha Species of Group 1

Adult Male

a. Large setae of third antennal segment arranged in rather definite transverse rows; basal third of segment dorsally with a number of small setae.
b. Small setae at base of third segment dorsally arranged in a loose cluster ---------- *?contrahens* Walker
bb. Small setae at base of third segment dorsally arranged in a fairly definite transverse row ---------- *corpulenta* (Kuwana)
aa. Large setae of third antennal segment, while definitely grouped in three regions, not arranged in any distinct transverse rows.
c. Bifurcate setae very few on anterior femora (perhaps not more than three on each); antennae, legs, and body relatively stout; penultimate pair of marginal tassels short and stout ---------- *pinicola* (Kuwana)
cc. Bifurcate setae more numerous (around one dozen or more); antennae, legs, and body relatively slender; penultimate pair of marginal tassels slender, proportionately much longer ---------- *howardi* (Kuwana)

GROUP 2. SPECIES OF THE ORIENTAL REGION

The included species, valid or otherwise, are: *benguetensis* (Cockerell) (*33, p. 235*) (male only known), *burmeisteri* Westwood (*172, p. 22*), *dalbergiae* Stebbing (*160, p. 142*), *leachii* Westwood (*172, p. 22*), *lichenoides* Cockerell (*29, p. 142*) (=*townsendi*), *luzonica* (Cockerell) (*36, p. 334*) (=*townsendi*), *mangiferae* Green, in Stebbing (*160, p. 332*), *maskelli* Cockerell (*26, p. 717*) (larva only positively known), *octocaudata* Green (*66, p. 16*) (=*mangiferae*), *palavanica* Cockerell (*33, p. 235*) (male only known), *philippinensis* (Green) (*77, p. 1*) (male only known) (=*townsendi*), *quadricaudatus* Green (*65, p. 434*), *saundersii* Westwood (*172, p. 22*), *stebbingii* Stebbing (*160, p. 135*), *townsendi* Cockerell (*27, p. 127*), and *variegatus* Green (*65, p. 433*).

Of all these, the larva of *townsendi* only has been studied. Authentic adult females of *dalbergiae*, *mangiferae*, *octocaudata* (=*mangiferae*), *stebbingii*, and *townsendi* have been examined. Authentic adult males of *benguetensis*, *dalbergiae*, *luzonica*, *octocaudata*, *palavanica*, *philippinensis*, and *stebbingii* have been available.

As in the northern group of these species, precise separation is a matter of much difficulty. The keys offered below, based in part on the work of Green (*78, p. 336*), must be regarded as no more than possibly suggestive.

Keys to Drosicha Species of Group 2

Adult Female

a. Body appearing uniformly broadly elliptical, least length-width ratio 1 to 0.7, average about 1 to 0.75; dorsal and ventral hairs small and short as in *stebbingii*, middorsal about 12μ, midventral about 28μ; Philippine Islands ---------- *townsendi* (Cockerell)
aa. Body appearing more elongate-elliptical, highest length-width ratio 1 to 0.65, this attained through swelling of some segments beyond uniform body outline, average ratio about 1 to 0.58; dorsal and ventral hairs varying; India.
b. Body hairs actually and relatively small, middorsal about 17–18 μ, midventral about 32μ; India on Shorea ---------- *stebbingii* (Stebbing)

bb. Body hairs much larger, middorsal about 35μ up to 80μ or more, midventral from about 65μ to 100μ or more.
c. Body hairs of moderate length, middorsal 35μ to 40μ, midventral 78μ to 93μ, but marginal long, about 110μ to 115μ, the larger marginal hairs therefore about three times the length of the average dorsal ones ..... *dalbergiae* (Stebbing)
cc. Body hairs longer, middorsal minimum about 45μ, midventral minimum about 74μ, marginal maximum about 111μ, the larger marginal not more than twice the length of the average middorsal ..... *mangiferae* (Green)
(*octocaudata* Green a synonym)

As in the preceding section, and with the other stages, the adult males are separable only with much difficulty, and the key given below is likewise intended as tentative and suggestive only.

Adult Male

a. Abdomen with two pairs of well-developed marginal tassels.
b. Apical marginal tassel about 1.14 mm. long, preapical correspondingly elongate ..... *variegatus* (Green)
bb. Apical marginal tassel about 0.5 mm. long, preapical about 0.36 mm. long ..... *quadricaudatus* (Green)
aa. Abdomen with more than two pairs of well-developed marginal tassels.
c. Indian species.
d. Penis sheath relatively short, expanded anterior portion narrow, corners of anterior end rounded, not at all angulate, constricted apical section relatively and actually stout; with three pairs of marginal tassels ..... *stebbingii* (Stebbing)
dd. Penis sheath more elongate, expanded portion broader, the corners of the anterior end tending to be rather distinctly angulate, constricted apical portion relatively much and actually somewhat more slender; with more than three pairs of marginal tassels (some individual examples apparently an exception to this).
e. Third antennal segment with about 36 setae in the intermediate whorl; abdomen with four pairs of tassels, the anterior long; bifurcate setae on anterior femora about 40 to 45 ..... *dalbergiae* (Stebbing)
ee. Third antennal segment with around 20 to 28 setae in the intermediate whorl, tassels varying; bifurcate setae varying.
f. Third antennal segment with about 25 to 28 setae in the intermediate whorl; abdomen with four or five pairs of tassels, the anterior pair, when in four pairs, well developed and elongate; bifurcate setae on anterior femora about 45 to 55.
fleachii (Westwood)
ff. Third antennal segment with about 20 setae in the intermediate whorl; abdomen with four pairs of tassels, the anterior quite short; bifurcate setae on anterior femora about 30 to 35 ..... *mangiferae* (Green)
(*octocaudata* Green a synonym)
cc. Philippine species.
g. Abdomen with six pairs of marginal tassels (not five pairs as stated in original description) ..... *palavanica* Cockerell
gg. Abdomen with not more than four pairs of marginal tassels.
h. Anterior pair of tassels relatively long and conspicuous; all tassels fairly evidently chitinized, blackish in color (*luzonica* Cockerell is a synonym) ..... *townsendi* (Cockerell)
hh. Anterior pair of tassels relatively short, inconspicuous; tassels not chitinized or blackish ..... *benguetensis* Cockerell

Genus Drosichoides Morrison

(Pl. 6, B, and figs. 87 and 88)

The writer recently erected this genus (*136, p. 106*) for the reception of two interesting East Indian male coccids.

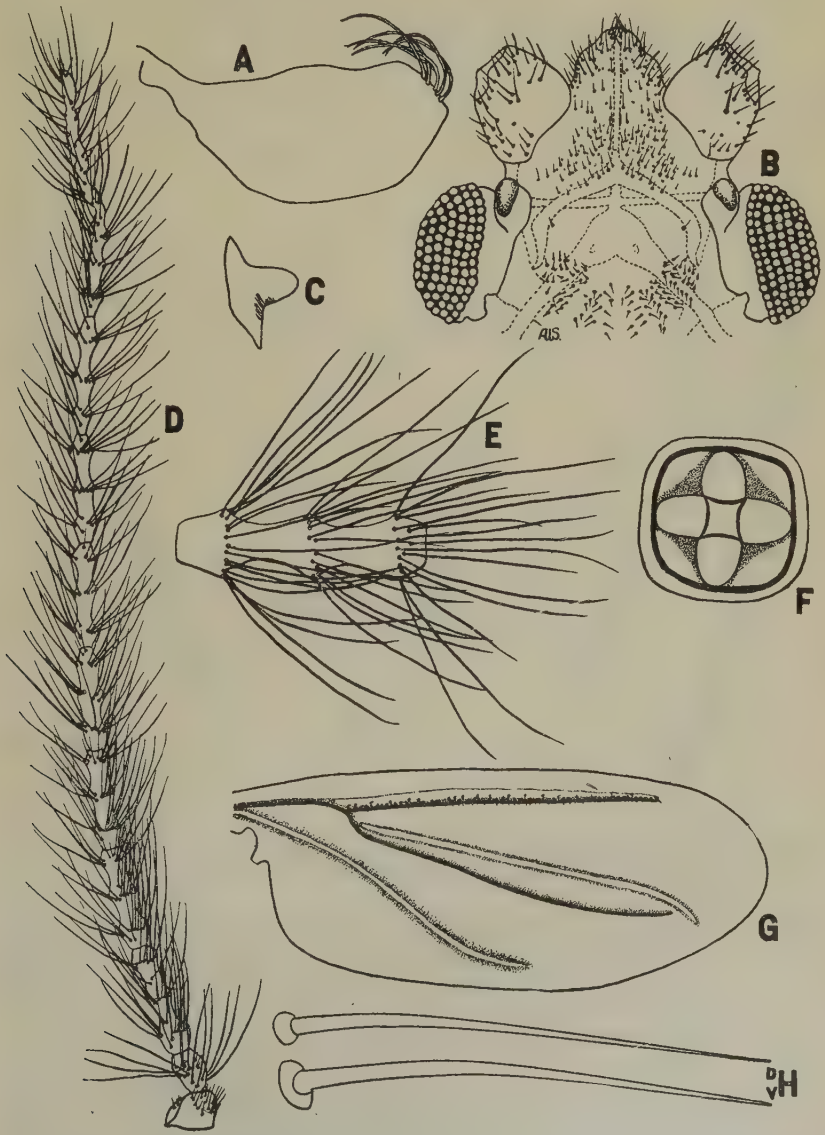

Fig. 87.—*Drosichoides haematoptera,* adult male: A, halter, × 60; B, head, dorsal, × 26.5; C, tubercle on head, × 650; D, antenna, × 12; E, third antennal segment, × 30; F, abdominal disk pore, × 1,500; G, wing, × 7.5; H, abdominal setae, dorsal (D) and ventral (V), × 650

GENERIC CHARACTERISTICS

Habit.—Uncertain.

Adult male.—Of the usual elongate shape; size large, resembling Drosicha in general appearance; head triangular in outline anteriorly, the ventral face of this portion with small tubercles; antennae longer than body proper, each

segment beyond second with three whorls of long setae, apical segment twice as long as preapical; wings much as in Drosicha, the basal diagonal vein nearly attaining the wing margins, but with the broad costal area bright red in color; halteres with several long, curved, knobbed setae at apices; anterior femora with bifurcate setae, each trochanter with several sensory pores; apex of abdomen with several (three pairs) long fleshy tassels; abdomen with transverse bands of slender setae and of quadrilocular disk pores; abdominal spiracles in seven pairs, not with definite circular chitinized collar, but each with an irregularly chitinized tube with the opening almost slitlike and bearing one or more conical teeth; penis sheath stout conical, apex bluntly rounded, hardly constricted before the apex, in contrast to Drosicha, and cleft ventrally to the slightly notched apex.

No other stages of any species of this genus are known.

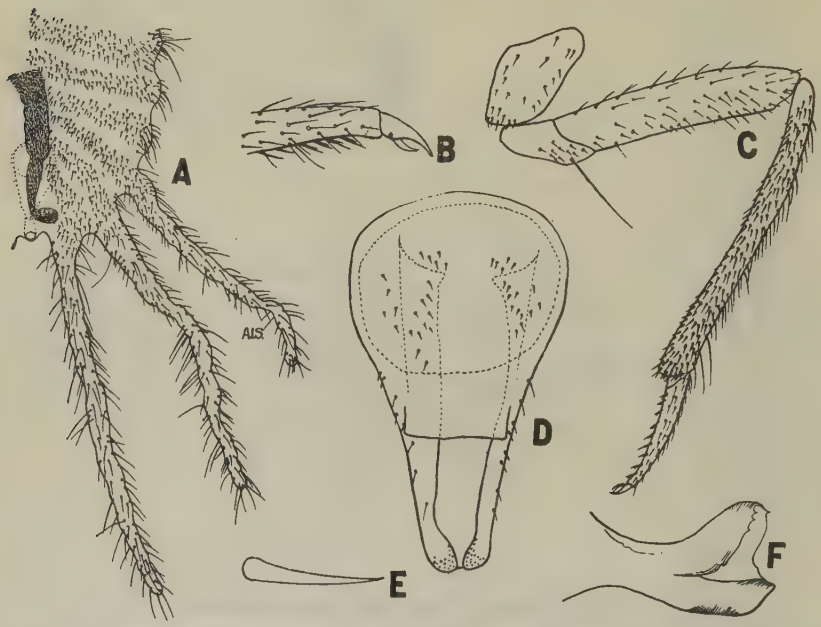

FIG. 88.—*Drosichoides haematoptera*, adult male: A, posterior apex of abdomen, dorsal, × 12; B, apex of tarsus and claw, × 60; C, leg, × 17.5; D, penis sheath, ventral, × 60; E, spine from penis, × 650; F, abdominal spiracle, × 530

It is considered that the shape and character of the development of the penis sheath, the bright red costal margin of the wing, and the very elongate terminal antennal segment all have some generic significance here. Perhaps the light reddish color of the legs and antennae is also significant in contrast to the dark or black of these parts in Drosicha.

The two species included, *haematoptera* (Cockerell) (*34*) from Borneo, and *sanguinea* (Cockerell) (*32*) from Palawan Island, have been separated in a key given by Professor Cockerell in the first paper cited. The differences in color and size between these, to which Cockerell calls attention in this key, certainly are plainly evident in the type specimens; no definite morphological differences, which would serve to differentiate the two species sharply, can be discerned in the unmounted type specimens.

TRIBE MONOPHLEBULINI MORRISON

This tribe has been erected (*136, p. 106*) for the two Australian genera Monophlebulus and Nodulicoccus, which, from our present limited knowledge, seem to form a natural group within the subfamily Monophlebinae.

TRIBAL CHARACTERISTICS

Habit.—Living during the growing period exposed on the bark or branches of the host, or beneath the loose bark of the host, or, rarely, beneath the ground on the roots of the host; probably always secreting a quantity of white fluffy matter at oviposition.

Adult female.—Body elliptical, length range extensive (7 to 22 mm.); derm membranous to more or less chitinized; antennae seven-segmented to nine-segmented, not unusual; legs stout, mostly with spinelike setae beneath, no claw denticles, digitules not exceeding claw apex, pointed at tips; beak small, stout conical, indefinitely two-segmented, the apical sensory setae acute at tips; thoracic spiracles stout, with bar and cluster of disk pores at opening; abdominal in seven pairs, much smaller, tubular with ring or collar of disk pores around opening; derm pores of the ordinary multilocular disk type, flat, trilocular, quadrilocular, or quinquelocular, some species in addition with large trilocular tubular pores with deeply invaginated centers; derm bearing spines, hairs, and setae, these all showing evident variation in shape, size, and abundance; anal tube with a band of polygonal wax pores at inner end, the derm area adjacent to the opening with the dermal appendages specially grouped or not; ventral cicatrices varying, either very numerous and in transverse segmental rows or in a single curved row behind the genital opening, but in any case without a median posterior one.

Preadult female.—In general resembling the adult rather closely.

Larva.—Shape more or less elongate elliptical; derm membranous; antennae five-segmented; legs slender, not unusual, claw irregularly faintly denticulate, digitules not exceeding apex of claw, pointed at tips; beak small, very stout conical, indefinitely two-segmented, the apical sensory setae acute at tips; thoracic spiracles large, with bar; abdominal very much smaller, without pores, simple tubular; derm pores including a small trilocular and a small multilocular disk type and, in one genus at least, a large trilocular tubular, deeply invaginated type; body with stout spines of varying shapes dorsally and laterally and with setae, with only a single pair of apical setae differentiated; anal tube with a band of wax pores at its inner end and a circle of disk pores near the opening; lateral ventral cicatrices only present, the median lacking.[28]

Adult male (based on representatives of only one genus).—Body elongate, apex of head triangular in outline; antennae 10-segmented, each segment beyond second bearing two whorls of long setae, apical distinctly longer than others; legs slender, anterior femora without bifurcate setae; wings somewhat narrowed, basal diagonal vein short, not approaching the wing margin; halteres elongate, with several curved setae at apices; apex of abdomen with one or more pairs of fleshy marginal tassels and with the margins of other abdominal segments protruding more or less conspicuously; penis sheath long conical, tapering gradually to apex, not sharply constricted; with seven pairs of abdominal spiracles, the anterior poorly developed; only the usual quadrilocular (or trilocular) type of derm pore present.

The known distribution of the species definitely included here covers only the Australian Continent and so only the Australian subregion of the Australasian region.

There is no information available regarding the biology of the included species. Maskell's experience (*124, p. 48, 51*) with adult females of *Monophlebulus crawfordi* forwarded to him in a living condition from Australia suggests that there might be a two-year

[28] This may prove incorrect, as the condition in the larva of Nodulicoccus can not be determined from the available material.

cycle with these species, although it seems more probable that there is normally one generation yearly, with overwintering in the egg stage.

Two genera are included here, Monophlebulus Cockerell and Nodulicoccus Morrison. The different stages of these, so far as known, may be separated by the following keys:

Keys to Genera of Monophlebulini

ADULT FEMALE

a. Ventral cicatrices small, very numerous, in ventral transverse rows on the abdominal segments and often on the thorax and head; anal opening not surrounded by a collar of small, closely set hairs; derm usually with some large tubular trilocular pores with deeply invaginated centers in addition to the usual types of disk pores ..... Monophlebulus

aa. Ventral cicatrices somewhat larger, relatively very few, at most in a single curved row behind genital opening; anal opening surrounded by a collar of small, closely set hairs; large trilocular tubular pores lacking ..... Nodulicoccus

LARVA

a. Dorsally and at margins with longitudinal rows of rather stout spines; margin with a single row of large trilocular tubular pores ..... Monophlebulus

aa. Dorsally and at margins with numerous buttonlike or fingerlike tubercular spines not in definite rows; no large trilocular tubular pores along margin ..... Nodulicoccus

The adult male stage of Nodulicoccus is not known.

Genus Monophlebulus Cockerell

(Pl. 6, C, and figs. 89, 90, 91, 92, and 93)

This genus was established by Cockerell (*23, p. 233*; *24*) in 1902 for the reception of monophlebine coccids having seven-segmented antennae in the adult female. While the basis for the erection of the genus is worthless taxonomically, the unit itself is a natural and a valid one.

GENERIC CHARACTERISTICS

Habit.—As given for the tribe.

Adult female.—Elongate elliptical, covered with more or less loose white secretion usually containing numerous glassy threads; antennae seven-segmented to nine-segmented, tapering, terminal longest; legs well developed, stout, the tarsus, tibia, and, in some species, the femur, bearing numbers of stout spinelike setae, these less developed in one species; beak indistinctly two-segmented, short and stout, apical sensory setae pointed at tips; thoracic spiracles large; abdominal spiracles in seven pairs, cylindrical, and each with a cluster of pores around the opening; derm usually with large tubular trilocular ducts (responsible for the glassy threads of the secretion), with one to three sorts of multilocular disk pores, these usually different dorsally and ventrally, and at least one sort relatively abundant; with scattered, long, slender setae set in conical bases, varying greatly in size but largest along body margin; usually with very numerous, closely crowded, long tapering, sharply pointed hairs, relatively few in one species, these hairs usually largest along body margin; with or without lanceolate or cylindrical spines; anal tube with a heavy band of polygonal wax pores at its inner end; ventral cicatrices small, circular, very numerous, arranged in transverse rows across the abdominal segments anterior to the genital opening.

Preadult female.—In general resembling the adult rather closely.

Larva.—Elongate elliptical; antennae five-segmented; legs normal, slender, claw with one pronounced and one or two obscure denticles, claw digitules

FIG. 89.—*Monophlebulus crawfordi,* adult female: A, outline, optical section, × 4; B, antenna, × 57.5; C, section of ventral abdominal derm, × 220; D, thoracic and abdominal spiracles, × 57.5; E, abdominal spiracle, × 220; F, base of largest type marginal seta, × 650; G, beak, × 60; H, leg, × 57.5; I, anal tube, × 60, with detail of polygonal wax pores, × 230; J, section of ventral derm, × 220, with detail of spine, × 640; K, marginal seta base, × 650; L, section of marginal derm, × 220, with detail of spine, × 640; M, section of dorsal derm, × 220, with detail of spine, × 640; N, small portion of one row of ventral cicatrices, × 57.5; O, dorsal hair, × 650

hairlike; number of spiracles as in adult, but these without pores and the contrast in size between thoracic and abdominal much more pronounced; derm with a marginal row of 13 to 14 pairs of large trilocular tubular pores, and with disk pores in longitudinal rows; with longitudinal bands of stout, cylindrical or lanceolate spines and with similar rows of slender setae; anal tube with a collar of wax pores at inner end and a ring of disk pores at opening; with four pairs of small, circular, ventral cicatrices.

Adult male.—Elongate, parallel-sided; apex of head triangular in outline; antennae 10-segmented, each segment beyond the second with two whorls of long setae, apical segment distinctly but not conspicuously longer than preceding; legs slender, without bifurcate setae on the anterior femora, these present on all tibiae and tarsi, claw without distinct denticles, digitules not exceeding apex, acute at tips; wing somewhat narrowed, the basal diagonal vein not approaching the margin; halteres elongate, with three to six curved setae at apex of each; apex of abdomen with at least one and usually more

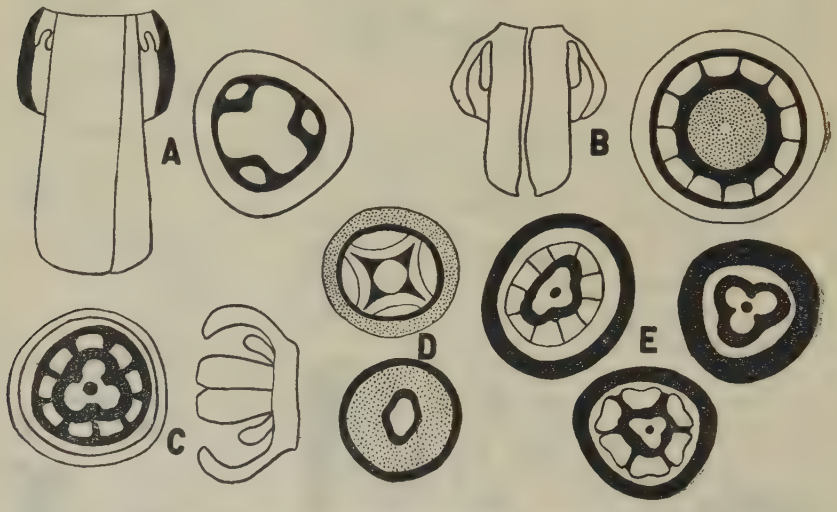

FIG. 90.—*Monophlebulus* spp., adult females: Multilocular disk pores, all × 1,500, A, *crawfordi*, long tubular trilocular, surface and section; B, *pilosior*, multilocular invaginated, surface and section; C, *crawfordi*, multilocular disk, surface and section; D, *pilosior*, surface, same pore at two levels, showing variation in appearance; E, *comperei*, surface, showing three varieties

pairs of well developed marginal tassels, and with the margins of the antepenultimate and even of other anterior segments more or less protruding; penis sheath nearly uniformly conical, not suddenly constricted near apex; with seven pairs of abdominal spiracles, the last two or three each with well defined collar at opening, the remainder poorly developed, hardly more than slits in the side of the abdomen; derm pores of the quadrilocular disk type.

On the basis of our present knowledge, the genus is exclusively Australian in its geographic distribution.

Nothing is known in detail regarding the life history of the included species.

Five species in all have been assigned to this genus. These have been figured and described in some detail and separated by a key not repeated here, included in a recent paper (*138, p. 6*).

Genus Nodulicoccus Morrison

(Pl. 6, D, and figs. 94 and 95)

This genus was only recently established by the writer (*138, p. 19*) for the species described by Maskell as *Monophlebus crawfordi* variety *levis*.

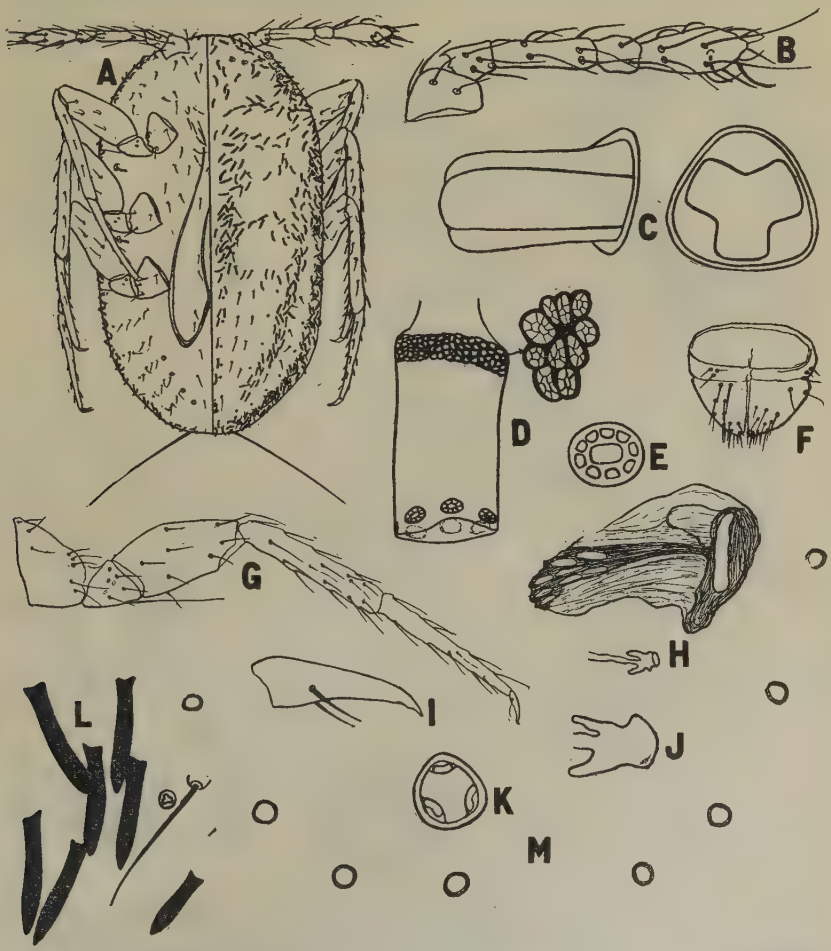

Fig. 91.—*Monophlebulus crawfordi* (except G), larva: A, outline, dorsal and ventral, × 57.5; B, antenna, × 115; C, marginal tubular pore, × 1,500; D, anal tube, × 335, with detail of polygonal wax pores, × 1,000; E, pore from anal tube, × 1,500; F, beak, × 115; G, *M. fuscus*, leg, × 115; H, thoracic and abdominal spiracles, × 460; I, claw, × 640; J, abdominal spiracle, × 1,500; K, disk pore, × 1,500; L, portion of dorsal derm, × 500; M, ventral cicatrices, × 330

GENERIC CHARACTERISTICS

Habit.—Uncertain, probably as given for the tribe.

Adult female.—Oval and broader behind to elliptical; derm membranous to distinctly chitinized and areolated; antennae nine-segmented, tapering strongly; legs normal, stout, the setae on the under side of the parts spinelike; beak incompletely two-segmented; with two thoracic and seven abdominal pairs of

spiracles, the former with a cluster of pores at opening of each, the latter with a band of pores around opening of each; derm pores of two sorts, triangular and multilocular disk with triangular or oval centers; derm with very stout, rounded, conical spines dorsally and somewhat longer and more slender spines with rounded tips laterally and ventrally; derm setae of two sorts, stout, tapering but with bluntly rounded tips, not very long, and normal, slender, tapering, acute setae; anal tube short, with a band of polygonal wax pores at inner end and a band of small hairs at opening and with a circle of much larger

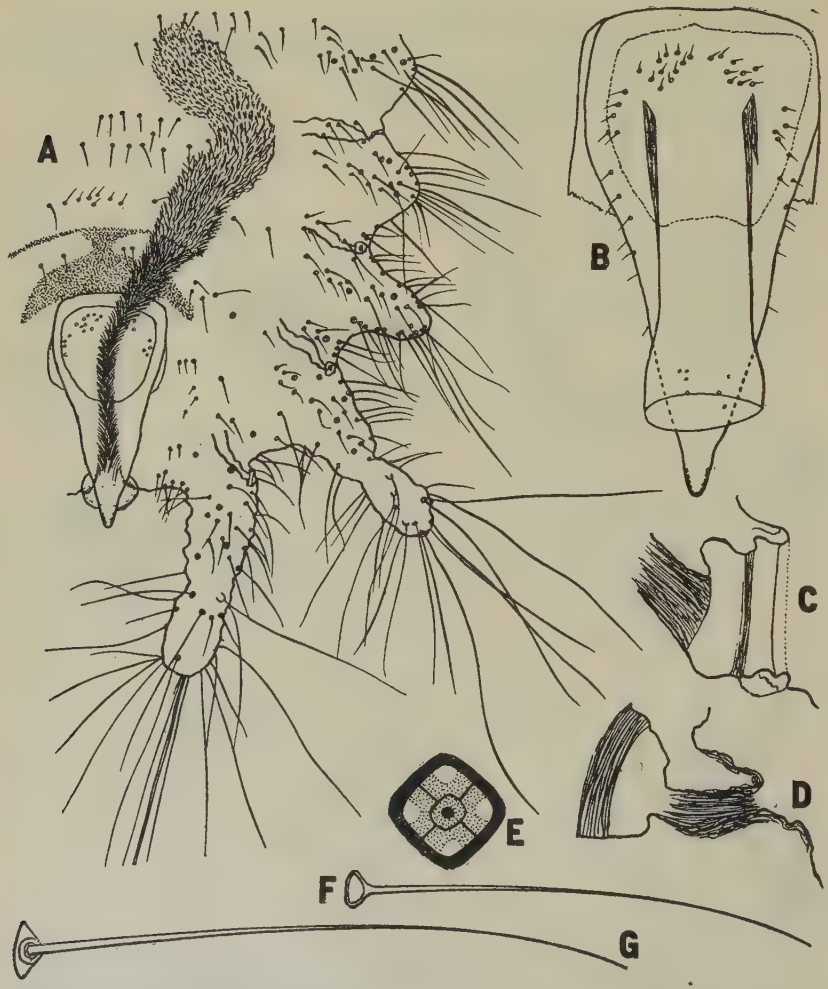

FIG. 92.—*Monophlebulus crawfordi* (except E), adult male: A, apex of abdomen, × 60; B, penis sheath, × 120; C, posterior abdominal spiracle, × 530; D, anterior abdominal spiracle, × 530; E, *M. comperei*, abdominal disk pore, × 1,500; F, abdominal hair, × 650; G, abdominal seta, × 650

hairs outside of these; ventral cicatrices intermediate in number, arranged in a semicircle, the median lacking.

Larva.—Elongate; antennae five-segmented; legs slender, claw irregularly slightly denticulate within, digitules not exceeding apex of claw; beak stout conical, segmentation uncertain; all spiracles uncertain; derm pores dorsally trilocular disk, around anal opening multilocular disk, ventrally uncertain; body spines numerous, developed dorsally as small buttonlike or mushroomlike

tubercles, laterally as fingerlike tubercles; anal tube with a band of irregular wax pores at inner end and a circle of disk pores near opening; ventral cicatrices uncertain, apparently without a median cicatrix.

This genus is likewise, so far as known, exclusively Australian in its geographical distribution.

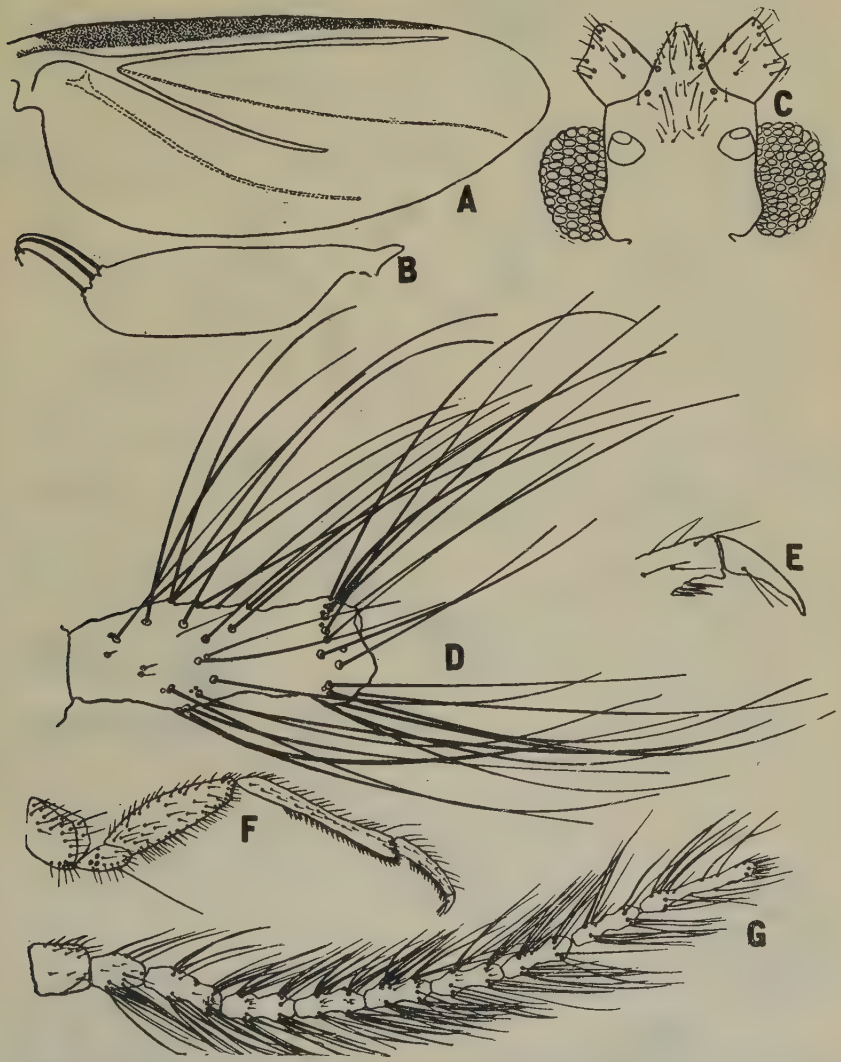

FIG. 93.—*Monophlebulus ?crawfordi* (except B and C), adult male: A, wing, × 12; B, *comperei*, halter, × 115; C, *comperei*, head, × 57.5; D, third antennal segment, × 120; E, claw, × 120; F, leg, × 30; G, antenna, × 30

Nothing is known regarding the details of the life history of the genotype.

TRIBE LLAVEIINI MORRISON

This tribe was recently established (*136, p. 106*) for the reception of three Neotropical genera.

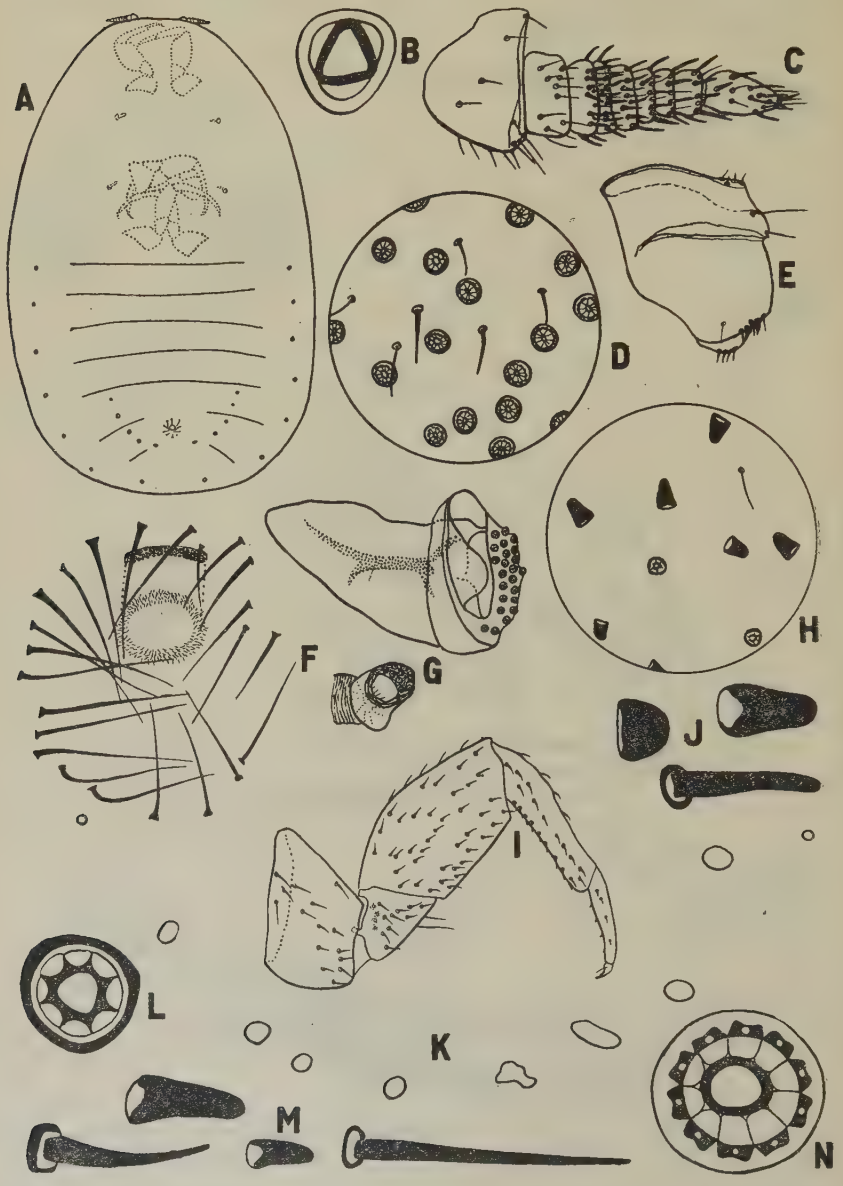

FIG. 94.—*Nodulicoccus levis*, adult female: A, outline, optical section, × 7.5; B, derm pore, × 1,500; C, antenna, × 60; D, section of ventral derm, × 220; E, beak, × 60; F, anal area, × 57.5; G, thoracic and abdominal spiracles, × 115; H, section of dorsal derm, × 220; I, leg, × 57.5; J, derm spines and seta, × 640; K, ventral cicatrices, × 30; L, disk pore, × 1,500; M, spines and setae, × 640; N, disk pore, × 1,500

TRIBAL CHARACTERISTICS

Habit.—Living exposed on the host plant during the growing period; secreting a mass of cottony matter forming a loose ovisac at oviposition time.

Adult female.[20]—Body elliptical; derm membranous; antennae 9-segmented to 11-segmented, tapering distinctly from base to apex; legs stout, the parts with more or less distinct spinelike setae beneath, claw stout, digitules not swollen at apices; beak stout conical, two-segmented, perhaps wanting occasionally; thoracic spiracles large, with broad bar and loose cluster of derm pores at opening; abdominal spiracles much smaller, in seven pairs, simple, short tubular, marginal; derm pores of one general type, this multilocular disk, with the size varying somewhat, the number of loculi varying considerably, range from about 9 to 16, and the centers varying from circular through elongate oval, triangular, trilocular, to as much as quinquelocular; derm bearing setae, hairs, and spines in varying numbers, or only setae and hairs; anal tube with somewhat

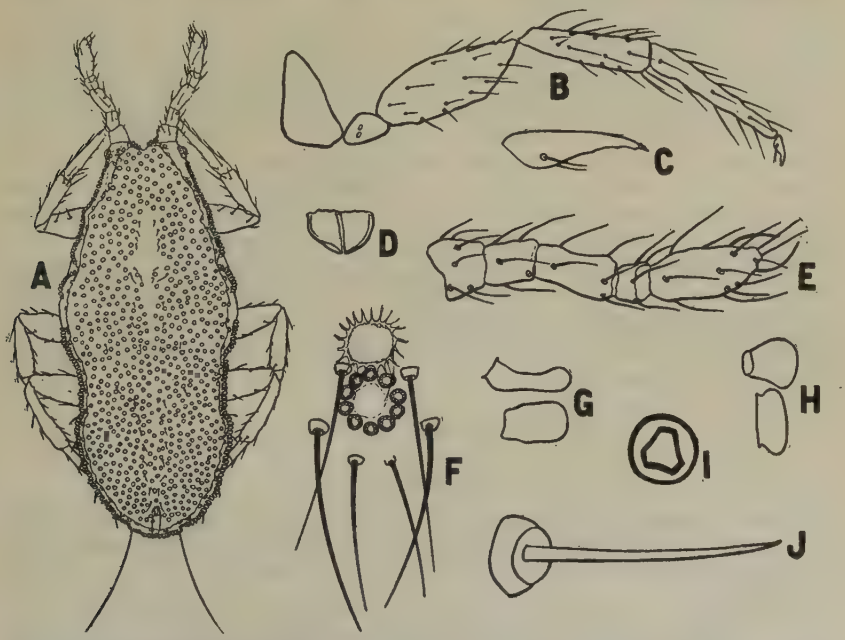

FIG. 95.—*Nodulicoccus levis*, larva: A, outline, dorsal, × 57.5; B, leg, × 115; C, claw, × 640. D, beak (outline only), × 115; E, antenna, × 165; F, anal tube, × 330; G, marginal spines, × 640; H, dorsal spines, × 640; I, disk pore, × 1,500; J, seta, × 1,500

chitinized ring at inner end, opening without or with a cluster of hairs, but without spines around it; ventral cicatrices varying in number from 3 to about 30, arrangement, where numerous, in a half oval with the posterior median behind the genital opening.

Intermediate female.—In general approaching the adult, but having the derm spines developed in numbers, fewer antennal segments, and other small differences.

Larva.—Elliptical, with long apical setae, lateral marginal setae of abdomen elongated or not; antennae six-segmented, the apical largest; legs not unusually slender; beak stout conical, two-segmented; thoracic and abdominal spiracles as in adult, the contrast in size more pronounced; derm pores of two sizes, quadrilocular or multilocular with circular center; derm with setae, hairs, and spines all present and in definite longitudinal rows, the spines showing reticulate areas toward bases; anal tube short, with band of polygonal wax pores at

[20] *Llaveia uhleri* (Signoret) does not fully accord with this diagnosis.

inner end, with or without ring of multilocular disk pores at opening; ventral cicatrices one to seven, if the latter, then arranged in a half oval.

Adult male.—Of the usual elongate shape, head triangular in outline anteriorly; antennae 10-segmented, the segments beyond the second trinodose, and each with three whorls of long setae, apical segment not evidently longer than preceding; legs slender, elongate, anterior femora and all tibiae and tarsi bearing numerous stout bifurcate setae, claws slender, not denticulate, claw digitules not swollen, not attaining apex of claw; wings not unusual, the costal margin bright red, the basal diagonal vein short, extending hardly more than half way to the wing margin; halteres large, flattened, with several knobbed and curved apical setae; abdominal spiracles fairly large, not heavily chitinized; derm pores of the one quadrilocular disk type only, rarely trilocular; derm setae slender; head also with small, nearly globular tubercles; apex of abdomen with more than one pair of long, marginal, fleshy tassels (three pairs constant ♂); penis sheath tapering gradually to a cylindrical tip.

The known distribution of the species definitely included here covers the Mexican and Antillean subregions of the Neotropical region, with possible lapping over into the Brazilian subregion, and doubtfully into the Rocky Mountain subregion of the Nearctic region.

There is no detailed information available regarding the biology of the included species. From the statements of Ibarra (*10, p. 201*) there appears to be a single generation yearly in *Llaveia axin* (Llave), with overwintering in the egg stage and growth in the female during the period from April to November, with the deposition of a large number of eggs (about 1,500) at maturity.

Three genera are included here, Llaveia Signoret, Protortonia Townsend, and a newly described genus, Llaveiella. The adult female and first larval stages of these may be separated by the keys given immediately below. The adult male stage is definitely known for only the one genus Llaveia.

Keys to Genera of Llaveiini

ADULT FEMALE

a. Ventral cicatrices numerous (15 to about 30), arranged in a half oval; setae on under side of femur, tibia, and tarsus conspicuously spinelike; anal opening not surrounded by a cluster of setae or of hairs and pores.

b. Antennae 11-segmented; no spines retained on body (spinelike hairs may be present); ventral cicatrices about 27 to 31 in number, more or less distinctly clustered; derm setae and hairs less abundant than disk pores ..... Llaveia

bb. Antennae nine-segmented; spines retained on body; ventral cicatrices about 15, not clustered; derm setae, hairs, and spines more abundant than disk pores ..... Llaveiella

aa. Ventral cicatrices reduced to three; setae on parts of legs not conspicuously spinelike; anal opening surrounded by a fairly well developed cluster of hairs accompanied by disk pores; antennae 11-segmented; spines wanting on body ..... Protortonia

LARVA

a. Lateral as well as apical marginal abdominal setae long and conspicuous; anal opening with a circle of disk pores.

b. Several ventral cicatrices (up to seven) ..... Llaveia

bb. A single median ventral cicatrix ..... Llaveiella

aa. Lateral abdominal marginal setae not developed as such, the apical pairs conspicuously longer; anal opening without a circle of disk pores; a single ventral cicatrix ..... Protortonia

Genus Llaveia Signoret

(Pl. 6, E, F, and figs. 96, 97, 98, 99, and 100)

The genus was established by Signoret (*158, p. 370*) in 1875 on the basis of his acquaintance with the published descriptions of *Coccus axin* Llave. In the same paper (*158, p. 351, 367*) the genus Ortonia was erected to include two newly described species, *O. bouvari* and *O. uhleri*. Subsequently (*16, p. 259*) Ortonia was shown to be preoccupied and at the same time it was shown that the species hitherto assigned to these two genera were really congeneric. It is necessary to point out here that Cockerell's conclusion to this effect is not precisely correct with respect to the specimens which he actually studied. His conception of *L. axin* was based on specimens which do not represent that species as it has been recognized by a series of Mexican and other writers (*2, 40, 41*), but rather on another, apparently undescribed species which must be assigned to a different genus. This species and genus are described in some detail below. The species here included in Llaveia are discussed after the generic diagnosis.

Generic characteristics

Habit.—As given for the tribe.

Adult female.—Body elliptical; derm membranous to more or less definitely chitinized, in the latter case each pore and seta base surrounded by a circular or oval, apparently unchitinized area; antennae 11-segmented, the basal segments broader than long, the remainder gradually narrowed to the apical, this distinctly longer than wide, the segments beyond the second each with one or more relatively stout, apparently sensory setae in addition to the normal slender type; legs large and stout, the coxa with three or more sensory pores on each face, the femora, tibia, and tarsus each with definite and conspicuous spinelike setae on the under half, claw digitules slender, tapering, not exceeding the claw, no denticle on claw; beak distinctly two-segmented, the apex bearing as many as 16 blunt-tipped sensory setae; thoracic spiracles stout and strongly chitinized, the derm pores more closely crowded adjacent to the opening but no pores definitely attached to the spiracle, conspicuously larger than the abdominal spiracles; these in seven marginal pairs, simple tubular with slightly enlarged atrium; derm pores fairly numerous, more abundant than setae and hairs, of one general multilocular disk type only, but exhibiting a considerable degree of variation with respect to number of loculi present in outer ring and shape of central area (see figures); body setae relatively few in number, small, some along margin much larger; body hairs smaller than average sized setae, more abundant but still not numerous, some, along margin and to a slight extent dorsally in one species, much stouter and definitely spinelike in appearance; the body spines so conspicuous in the larval and intermediate stages entirely wanting in the adult; anal opening not chitinized, not surrounded by a distinct cluster of setae and hairs or pores or both; anal tube simple, short, with somewhat chitinized band at the inner end but no internal pores; ventral cicatrices relatively numerous, placed only on the ventral surface of the abdomen, but retaining a semicircular arrangement, the total normal number ranging from 27 to 31.

Intermediate female.—In general resembling the adult, but with fewer antennal segments, fewer pores and setae, and, in contrast to the adult, with the conspicuous spines of the larval stage still present, particularly along the margin.

Larva.—Elliptical, the margin with a fringe of elongate setae, the apical pairs not differentiated in size from the remainder; antennae six-segmented, the segments relatively short and stout as compared with Icerya and related genera; legs not unusual, some of the setae along under side stout and almost spinelike, claw with denticle, claw digitules not exceeding claw apex; beak short conical, fairly distinctly two-segmented, with several (about 12) blunt-

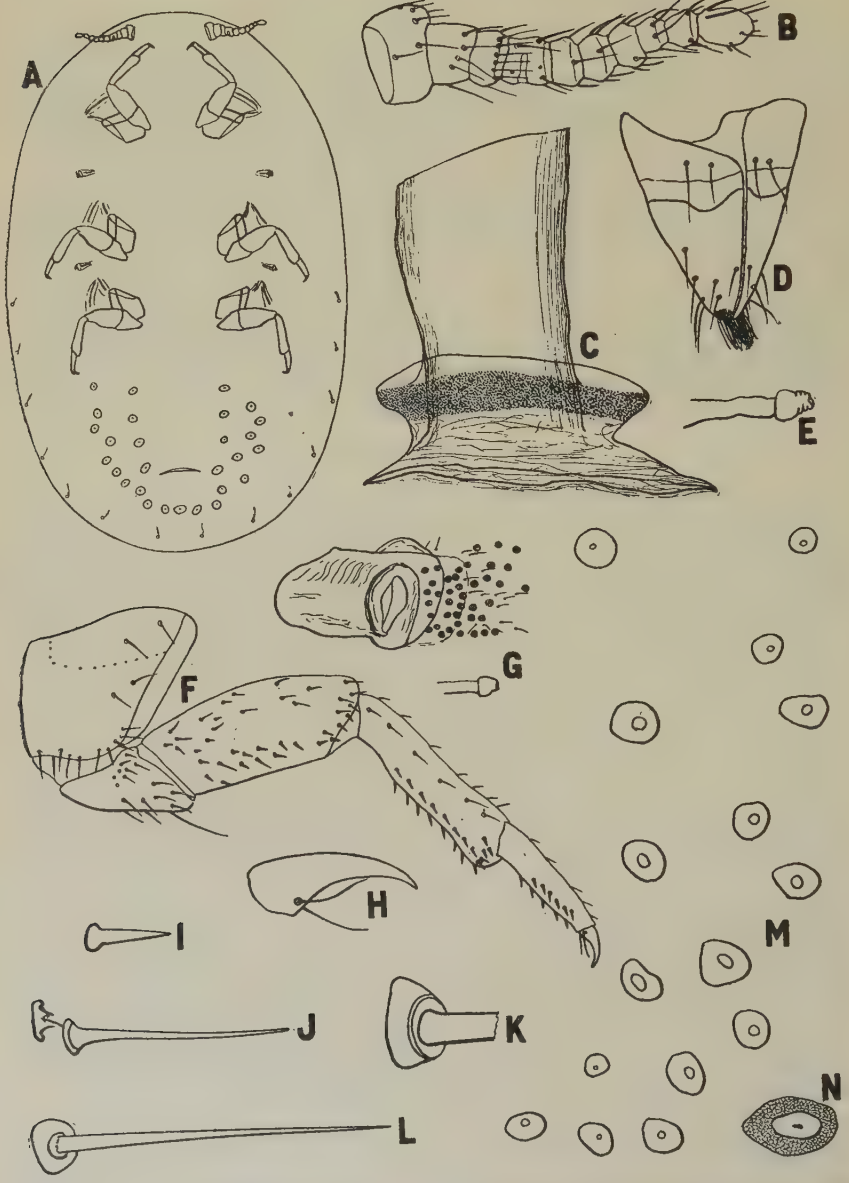

FIG. 96.—*Llaveia mexicanorum* (A, B, F, H, N) and *L. oaxacoensis* (C, D, E, G, I, J, K, L, M), adult females: A, outline, optical section, × 7.5; B, antenna, × 80; C, anal tube, × 60; D, beak, × 60; E, abdominal spiracle, × 120; F, leg, × 80; G, thoracic and abdominal spiracles, × 60; H, claw, × 115; I, stout lateral spinelike hair, × 650; J, normal dorsal hair, × 650; K, base of largest type marginal seta, × 650; L, normal dorsal seta, × 650; M, ventral cicatrices from one side of abdomen, × 30; N, detail of single ventral cicatrix, × 60

tipped sensory setae on apex; thoracic spiracles with chitinized bar much as in adult, very much larger than abdominal, these small, simple tubular, in seven pairs; derm pores of one simple multilocular disk type only, with from four to six loculi; derm bearing, in addition to the large marginal setae, dorsal

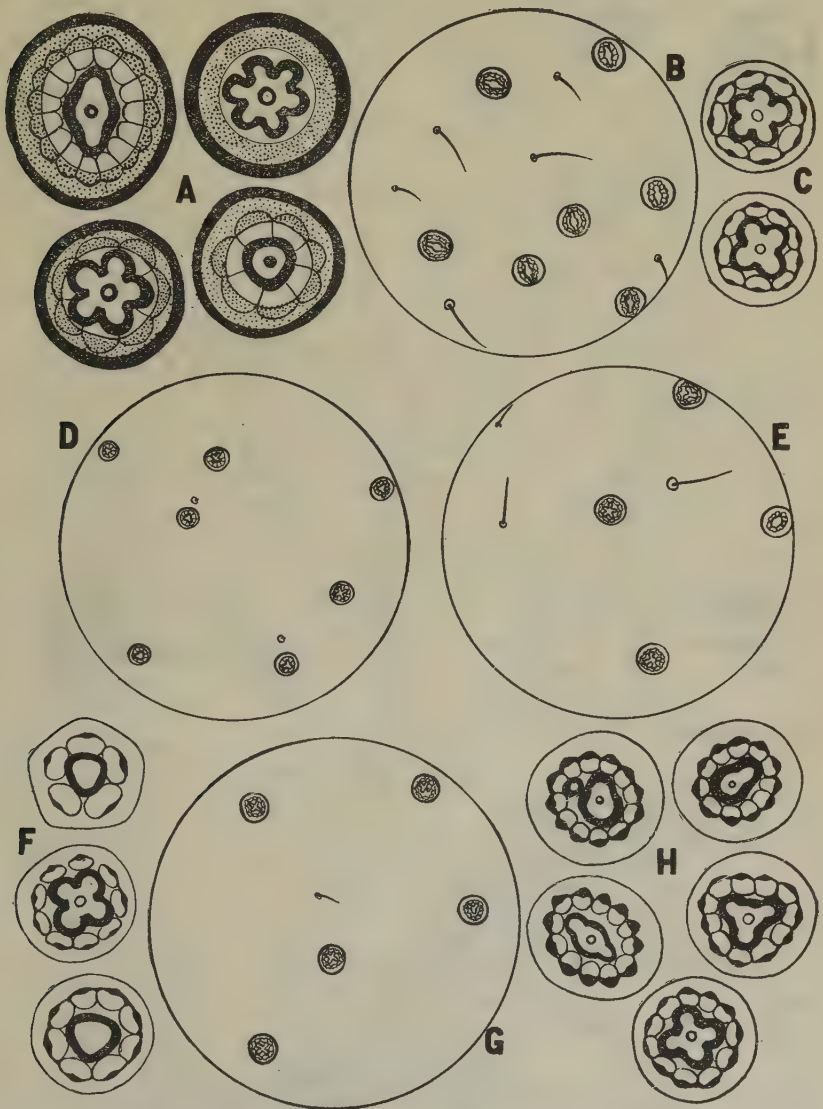

FIG. 97.—*Llaveia mexicanorum*, adult female: A and C, various sorts of derm disk pores, × 1,500; B, section of posterior midventral derm, × 230; D, section of middorsal derm, × 230; E, section of midventral derm, × 230; F, dorsal disk pores, × 1,500; G, section of posterior middorsal derm, × 230; H, ventral derm pores, × 1,500

and ventral rows of much smaller setae and hairs and, on the dorsum, median, two intermediate, and two marginal longitudinal rows of stout spines; anal tube with collar of disk pores just within the opening and with a double band of polygonal wax pores at inner end; with seven ventral cicatrices arranged in a half oval, one, the largest, median and posterior in position.

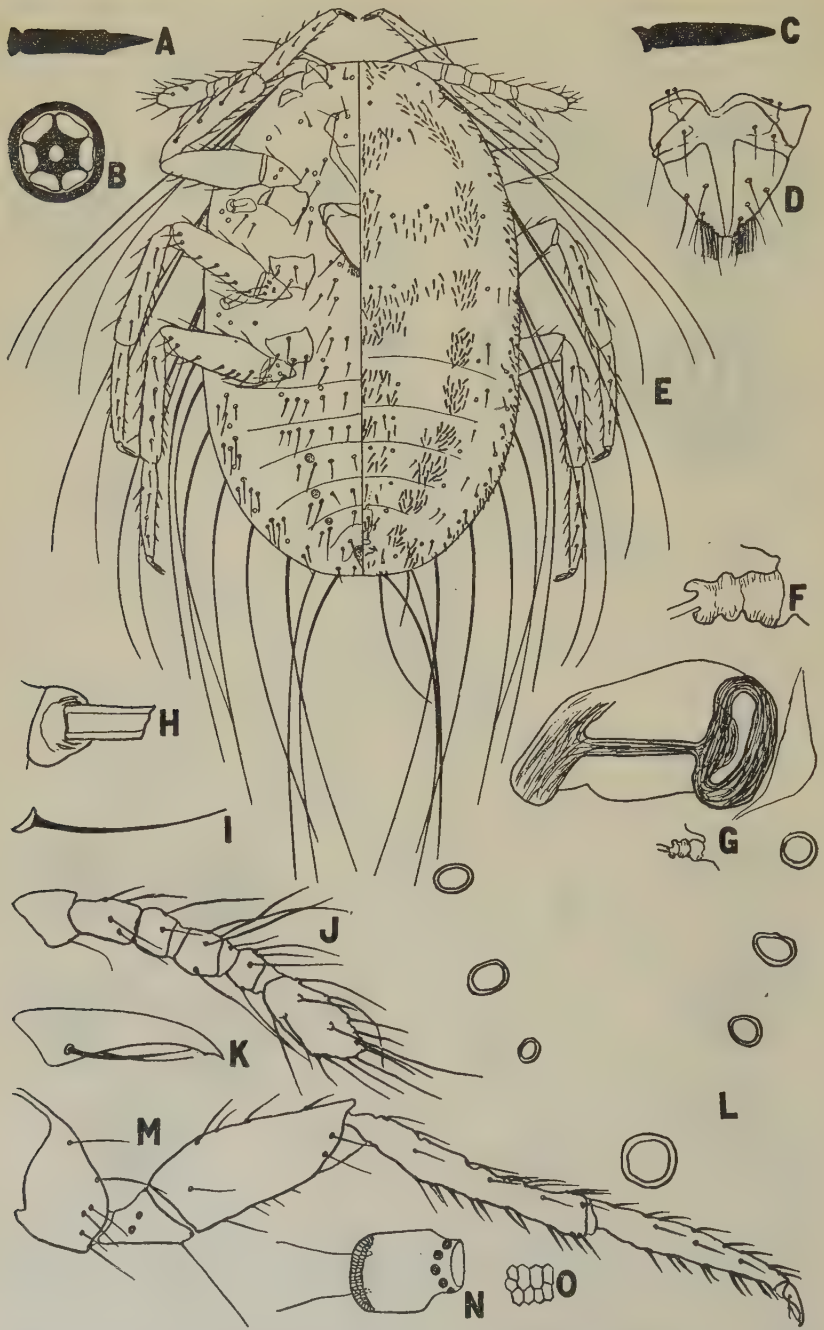

FIG. 98.—*Llaveia mexicanorum*, larva: A, spine from lateral row, × 650; B, derm pore, × 1,500; C, spine from median row, × 650; D, beak, × 115; E, outline, dorsal and ventral, × 60; F, abdominal spiracle, × 1,280; G, thoracic and abdominal spiracles, × 460; H, base of large marginal seta, × 650; I, ventral hair, × 650; J, antenna, × 115; K, claw, × 530; L, ventral cicatrices, × 650; M, leg, × 115; N, anal tube, × 230; O, detail of polygonal wax pores, × 650

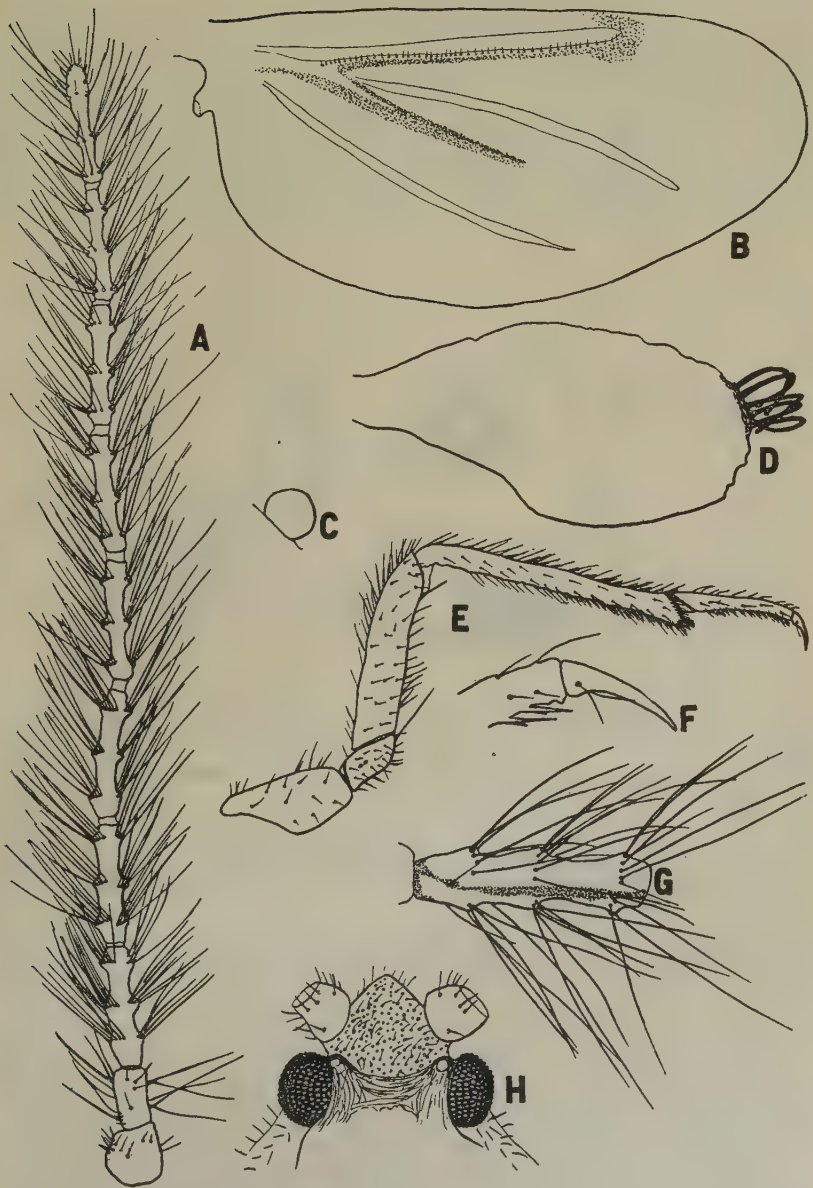

FIG. 99.—*Llaveia oaxacoensis*, adult male: A, antenna, × 30; B, wing, × 17.5; C, tubercle from apex of head, × 650; D, halter, × 120; E, leg, × 30; F, claw, × 120; G, third antennal segment, × 60; H, head, dorsal, × 30

Adult male[30] (generic characters based on one species only).—Body elongate, sides nearly parallel; apex of head triangular in outline, head bearing numerous pores, setae, and small globular protuberances; antennae approximately as long as body, 10-segmented, the segments beyond the second elongate, each trinodose and bearing three whorls of setae, the apical approximately as long as those preceding it; legs slender, bearing numerous setae, many on all the tibiae and tarsi and on the anterior femora stout, conspicuously unequally bifurcate, claw slender, claw digitules not exceeding apex; wings normal in shape, the basal diagonal extending only about half-way to the margin, and with the usual diagonal clear stripes; halteres flattened, broadened at apex, with five or six knobbed setae at apices; apex of abdomen with three pairs of long, marginal, fleshy tassels, all bearing numerous setae; penis sheath tapering strongly from base to near apex, the tip cylindrical, apex rounded and slightly cleft; abdominal spiracles simple, short tubular, in seven pairs; only the single quadrilocular disk type of pore present; body setae elongate and slender.

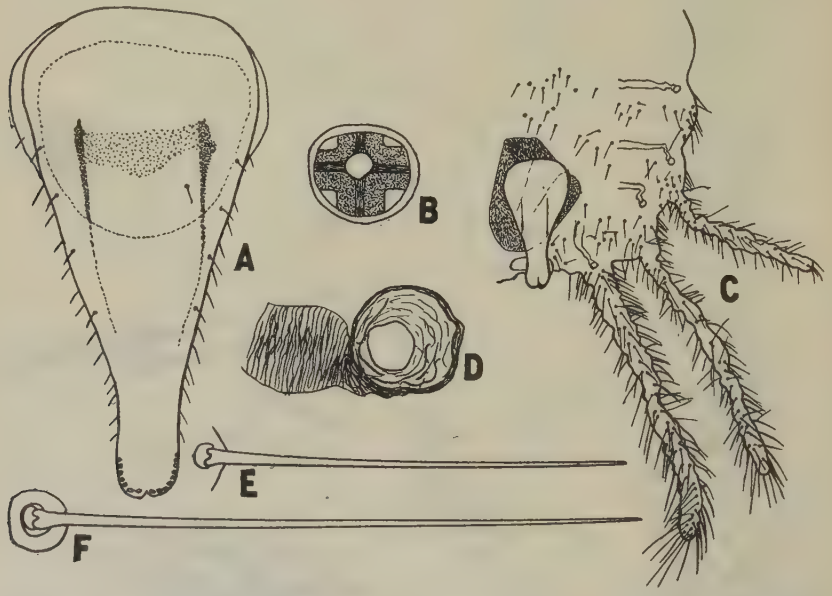

FIG. 100.—*Llaveia oaxacoensis*, adult male: A, penis sheath, × 120; B, abdominal disk pore, × 1,280; C, apex of abdomen, × 30; D, abdominal spiracle, × 1,280; E and F, abdominal setae, × 650

Altogether 14 species and subspecies have been assigned to this genus at various times. These have been disposed of as follows: *axin* Llave (*109, p. 147*), *bouvari* (Signoret) (*158, p. 368*), and *mexicanorum* (Cockerell) (*14, p. 437*) are retained in the genus and a previously apparently undescribed species, *oaxacoensis* Morrison, has recently been added to these (*136, p. 107*); *axin* variety *dorsalis* (Dugès) (*42, p. 160*), according to the description, is differentiated from typical *axin* only by the presence of irregular blackish markings dorsally and ventrally, its separate status seems doubtful, but no change can be made without a study of authentic specimens of the form; *benguetensis* Cockerell (*33, p. 235*) has already been

[30] Although it is true that Herrera (*99, p. 198*), as pointed out by Cockerell (*16, p. 259*), has stated that the male of *L. axin* has eight "cerdas terminales," in the same volume of La Naturaleza an article by Ibarra (*101, p. 200*) states precisely that in this stage of the male the abdomen is terminated by "seis hilos sedosos," which description agrees with this male.

transferred to the genus Drosicha, where it is given further consideration; *cacti* (Linnaeus) (*115, p. 457*) and *primitiva* (Townsend) (*164, p. 169*) have been transferred to the resurrected Protortonia and will be discussed in detail below; *callitri* Froggatt [31] is an Icerya closely related to *I. purchasi* Maskell; *haematoptera* Cockerell (*34*), *luzonica* Cockerell (*36, p. 334*), and *sanguinea* Cockerell (*32*) have already been included in the tribe Drosichini; *uhleri* Signoret (*158, p. 369*) is necessarily left unplaced, although the evidence now available indicates that it will eventually require the establishment of a separate genus for its reception; Vayssière has very recently (*170, p. 303*) placed his *Monophlebus dugesi* (*166, p. 335*) as a synonym of *L. axin* (Llave); and the final species included here, *saundersii* (Westwood) (*172, p. 22*), from the original description has been assigned to Drosicha, although the correctness of this placing is questionable.

The key given below includes only a part of the species that have been retained in the genus, and is highly unsatisfactory; it is included in the hope that it may serve to indicate probable species identities to other workers.

KEY TO SPECIES OF LLAVEIA

Adult female

a. Some of the body hairs along margin, and to some extent dorsally, stout and distinctly spinelike in form; length range of body 6 to 10 mm ..... *oaxacoensis* Morrison

aa. All of body hairs slender, actually hairlike.

b. Length range of body 7 to 12 mm ..... *mexicanorum* (Cockerell)

bb. Length range of body 16 to 25 mm ..... *bouvari* (Signoret)
axin (Llave)

If the general statement in literature to the effect that the length of *axin* is about 1 inch be accepted as precise, then no specimens of this species have been available for examination. It seems at least possible that *axin* varies considerably in length, and that *bouvari* is identical with it. To determine this positively would require an examination of full-sized specimens of *axin* from the type locality. Fragments of a single adult female of *L. uhleri* have been examined. These fragments indicate rather clearly that *uhleri* can not be considered a characteristic member of the genus, and that it will probably be necessary to erect a new genus for its reception when the availability of ample study material permits an elucidation of all of its characters.

GENUS PROTORTONIA TOWNSEND

(Figs. 101 and 102)

This genus was established by Townsend (*164, p. 169*) in 1898 as a subgenus of Ortonia, at that time supposedly with valid status as a coccid genus. Later it was first raised to generic rank by Cockerell (*18, p. 390*) and then suppressed in the Fernald catalogue (*46, p. 16*) as congeneric with Llaveia, which had supplanted Ortonia. A study of the genotype and of another included species of much historical interest appears to give ample grounds for its segregation as a valid

[31] This species was described in Froggatt's book, "The Forest Insects of Australia," published in 1923 (*57, p. 162*).

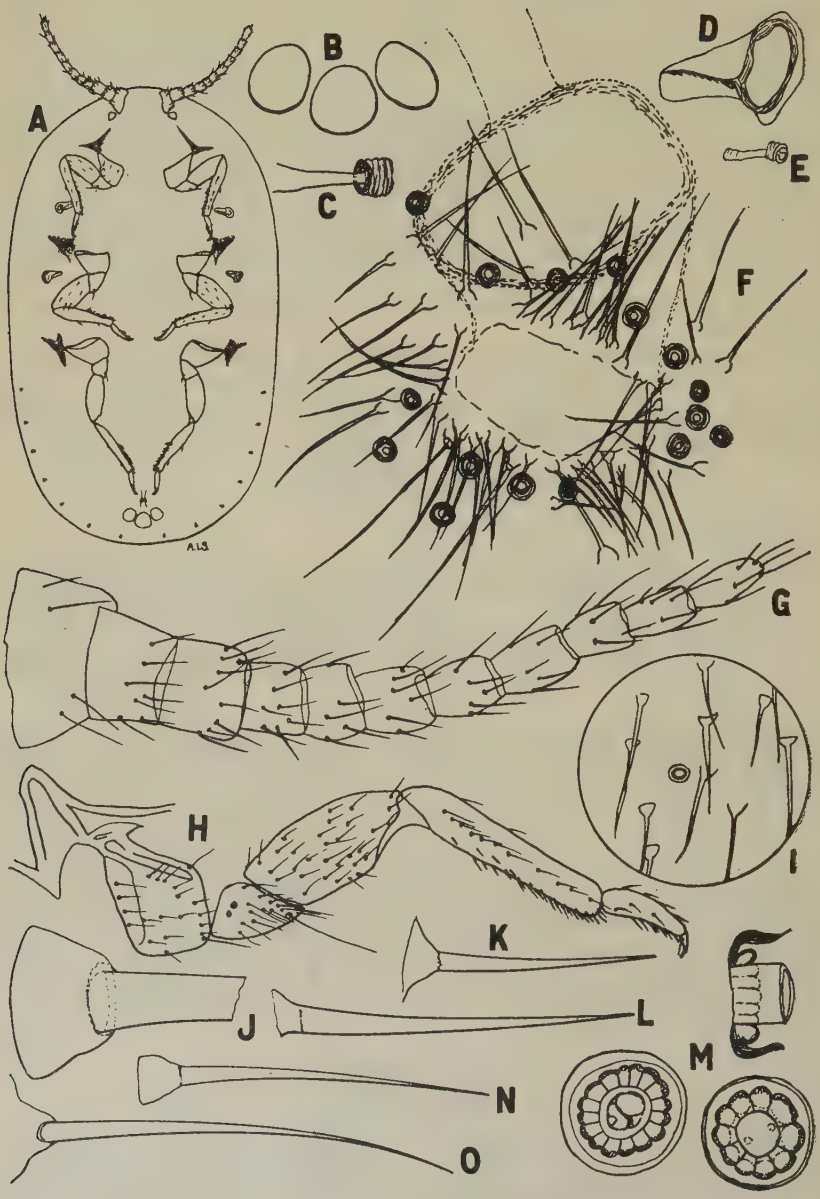

FIG. 101.—*Protortonia primitiva*, adult female: A, outline, optical section, × 7.5; B, ventral cicatrices, × 30; C, abdominal spiracle, × 120; D, thoracic spiracle, × 60; E, abdominal spiracle, × 60; F, anal area, × 230; G, antenna, × 60; H, leg, × 30; I, section of dorsal derm, × 220; J, base of largest type marginal seta, × 650; K, middorsal hair, × 650; L, midventral hair, × 650; M, derm disk pores, × 1,280; N, midventral hair, × 650; O, middorsal seta, × 650

generic unit. The genotype is the species *Ortonia primitiva* Townsend (*164, p. 169*) and the other species now definitely associated with it is the *Coccus cacti* of Linnaeus (*115, p. 457*) which, in the opinion of the writer, has been definitely rediscovered in the specimens that have been studied at this time.

GENERIC CHARACTERISTICS

Habit.—Not certain, probably as given for the tribe.

Adult female.—Body elliptical, about 6 to 8 mm. in length; derm membranous; antennae 11-segmented, segments broad at base, narrower toward apex, intermediate as well as apical bearing stout sensory setae as well as normal setae; legs stout, relatively and actually smaller than in Llaveia, the setae along the

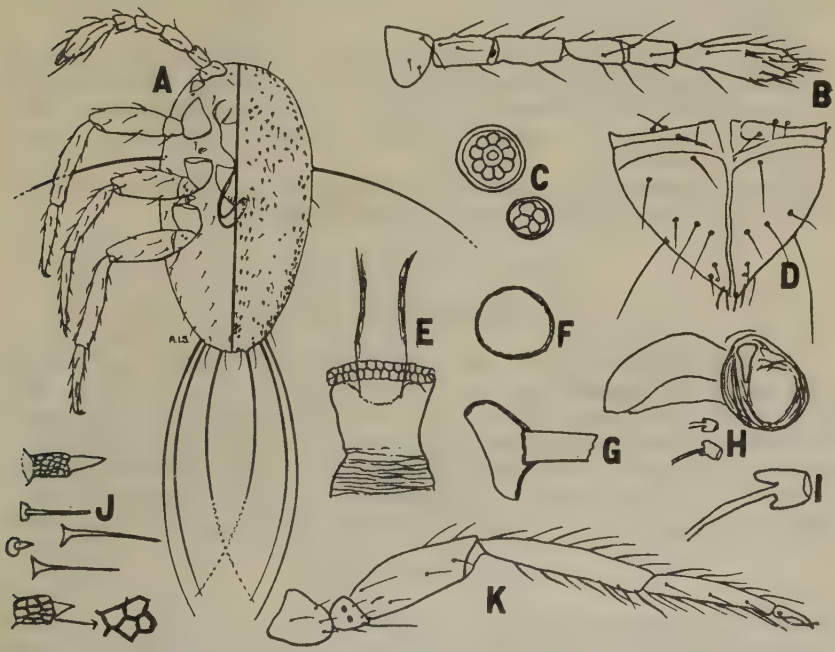

FIG. 102.—*Protortonia cacti*, larva: A, outline, dorsal and ventral, × 60; B, antenna, × 115; C, derm disk pores, × 1,280; D, beak, × 115; E, anal tube, × 330; F, ventral cicatrix, × 330; G, base of marginal seta, × 650; H, thoracic and abdominal spiracles, × 460; I, abdominal spiracle, × 1,280; J, spines, hairs, and setae, × 650, with detail of reticulation of spine, × 1,280; K, leg, × 115

underside, while stout, not distinctly spinelike, claw stout, digitules not exceeding apex, inner face sometimes showing a number of indistinct denticles; beak possibly stout conical, three-segmented;[32] thoracic spiracles large, with bar, abdominal in seven pairs, much smaller, short tubular, each with the inner end strongly constricted for attachment to the trachea; derm pores of the one multilocular disk type, of two sizes, the one slightly smaller with about 10 loculi, the other larger, with about 16 loculi, centers varying from circular through unequally bilocular to equally bilocular; derm setae and hairs not very large or stout, but relatively abundant as compared with Llaveia, and much more abundant than the pores, some setae, along body margin, much larger; no spines present; anal tube simple, short, with a simple chitinized ring at the

[32] The mouth parts and beak are not fully developed in any of the few adult female specimens of the two included species that are available for study, the condition suggesting that which is seen in some Margarodinae, but the evidence is unsatisfactory and leaves the impression of unfinished rather than incomplete development.

inner end, the external opening surrounded by a ring of hairs, accompanied by some pores, in contrast to the condition in Llaveia; ventral cicatrices three in number, large oval, placed beneath anal tube immediately behind genital opening.

Preadult female.—In general resembling the adult; the body hairs noticeably stouter, the marginal setae larger and more conspicuous; spines retained.

Larva (based on *cacti* only).—Elliptical, apex of abdomen with three pairs of long setae, remainder of margin without enlarged setae except one pair probably on mesothorax; antennae six-segmented, the setae on the apical segments short; legs slender, not unusual, claw with denticle and digitules exceeding tip; beak short conical, apparently two-segmented; thoracic spiracles much larger than abdominal; derm pores of two sorts, one quadrilocular, one multilocular; derm with rows of setae and hairs and, dorsally, a median and two submarginal rows of stout spines, constricted near apices and exhibiting a reticulated surface; anal tube with a band of polygonal wax pores at inner end, otherwise a simple tube; with a single, median, circular, ventral cicatrix.

Adult male.—Not definitely known.

The two included species, from the very limited study material available, appear to be quite closely related. No tangible differences have been observed in the adult females, excepting only that the hairs on the derm appear to average definitely shorter in length with *cacti* than with *primitiva.*

The known distribution of the genus includes the Mexican and the Antillean subregions of the Neotropical region.

Genus Llaveiella Morrison

(Pl. 7, A, and figs. 103 and 104)

The writer (*136, p. 108*) has just established this genus for the reception of the insect considered by Cockerell (*12, p. 271; 16, p. 259; 15, p. 2; 22, p. 79; 23, p. 233; 24, p. 319*) to be *Llaveia axin* (Llave). The genotype and only included species is *L. taenechina* Morrison, a new name proposed at the same place by the writer for the specimens from Salina Cruz, Mexico, collected by C. H. T. Townsend, May, 1896, and apparently incorrectly identified by Cockerell.

GENERIC CHARACTERISTICS

Habit.—Uncertain, probably as given for the tribe.

Adult female.—Body elliptical, length about 12 mm.; derm membranous or faintly chitinized at maturity; antennae normally nine-segmented, not so strongly tapering as in other related genera, the intermediate and apical segments all bearing obvious heavy sensory setae; legs stout, bearing well developed spinelike setae beneath as in Llaveia; beak short conical, fairly distinctly two-segmented, with 14 to 16 blunt-tipped sensory setae at apex; thoracic spiracles with bar and a cluster of pores adjacent; abdominal in seven pairs, much smaller, cylindrical, hardly constricted internally; derm pores distinctly of two sizes, the smaller with four to six loculi and a circular center, the larger with 9 to 14 loculi and trilocular, elongate, or multilocular centers; derm setae not abundant; derm hairs and spines relatively abundant as compared with Llaveia, this the only genus in the group retaining the spines in this stage; anal tube and opening similar to those in Llaveia; ventral cicatrices numerous (15 in genotype), set in a half oval row on the venter of the abdomen, the median posterior one much the largest.

Intermediate stages.—None available.

Larva.—Elliptical; antennae six-segmented, the setae on the apical segment long and conspicuous; legs large, slender, none of the setae spinelike; beak distinctly two-segmented, with several blunt-tipped sensory setae at apex; thoracic spiracles large, with broad bar; abdominal not located with absolute certainty,

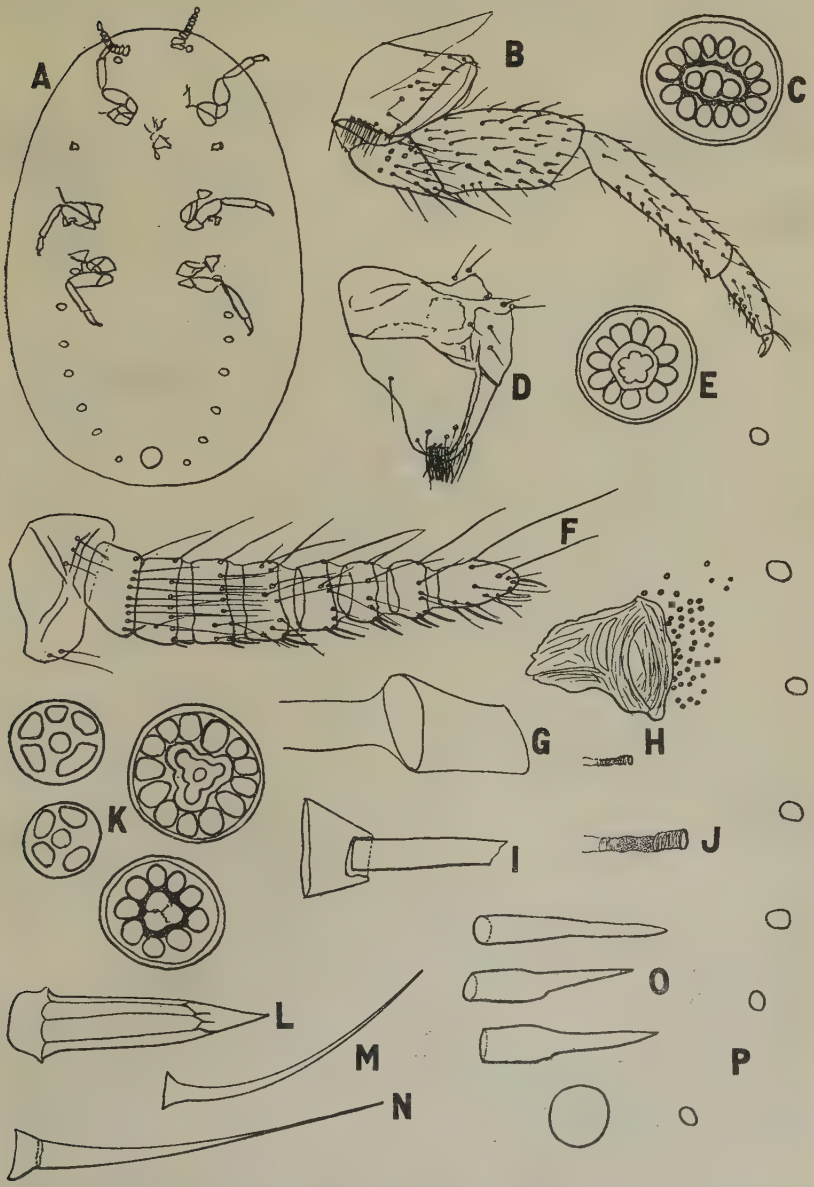

FIG. 103.—*Llaveiella taenechina*, adult female: A, outline, ventral, × 5.5; B, leg, × 30; C, disk pore, × 1,280; D, beak, × 60; E, spiracular disk pore, × 1,280; F, antenna, × 60; G, anal tube, × 60; H, thoracic and abdominal spiracles, × 60; I, base of largest type marginal seta, × 650; J, abdominal spiracle, × 120; K, derm disk pores, × 1,280; L, dorsal spine, × 1,280; M, ventral hair, × 650; N, dorsal hair, × 650; O, dorsal spines, outline, × 650; P, ventral cicatrices from one side of abdomen, × 17.5

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believed to be represented by very minute simple tubes; derm pores of two sorts, quadrilocular and multilocular, these last varying somewhat; derm setae and hairs present in rows; derm spines present dorsally in a marginal and intermediate longitudinal row on each side and a median row, these last plainly

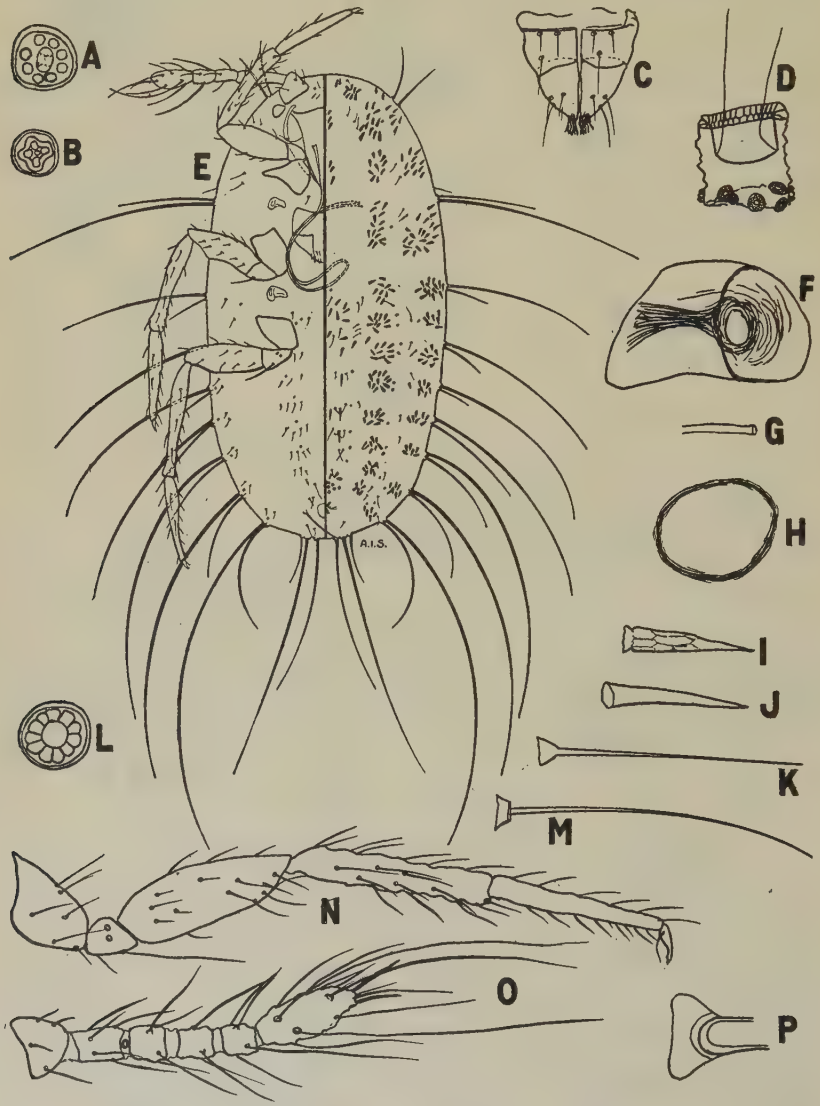

FIG. 104.—*Llaveiella taenechina*, larva: A, derm pore, × 1,280; B, dorsal derm pore, × 1,280; C, beak, × 115; D, anal tube, × 330; E, outline, dorsal and ventral, × 60; F, thoracic spiracle, × 460; G, abdominal spiracle, × 1,280; H, ventral cicatrix, × 330; I, spine from submarginal row, × 650; J, spine from median row, × 650; K, dorsal hair, × 650; L, disk pore from anal tube, × 1,280; M, dorsal seta, × 650; N, leg, × 115; O, antenna, × 115; P, base of marginal seta, × 650

differing in shape and appearance from those in the other rows; margin of abdomen with long curved setae in addition to the apical pairs; anal tube with band of polygonal wax pores at inner end and with loose collar of disk pores at opening; with a single ventral cicatrix.

As was already indicated, this genus is at present known only from the Mexican subregion of the Neotropical region.

TRIBE ICERYINI COCKERELL

This tribe, as established by Cockerell (*17, p. 274*) in 1899, was intended for the reception of all Monophlebinae excepting only the genus Monophlebus. In its present usage the limits of the tribe are much narrower, since it is confined, with a single exception, to Icerya and genera evidently quite closely related to it.

TRIBAL CHARACTERISTICS

Habit.—Living exposed on the host leaves, branches, or bark during the growing period; method of oviposition various, eggs deposited directly beneath body, in an ovisac, in a loose mass of secretion or in a marsupium within the body.

Adult female.—Body usually ovoid, broader behind, sometimes elliptical; derm membranous to definitely and even fairly heavily chitinized, at least dorsally and at maturity; antennae not unusual, elongate, tapering, 9-segmented to 11-segmented, the sensory setae not sharply differentiated; legs mostly of moderate size, the setae on the under side of some of the parts, in some species, fairly stout, somewhat spinelike, but not heavy and conspicuously spinelike; beak mostly very short and stout conical, apparently one-segmented, but elongated and fairly distinctly three-segmented in one genus, the apical sensory setae stout, truncate, to broadened, to slightly bifid at tips in all the genera; thoracic spiracles each with bar but without disk pore cluster at opening; abdominal spiracles in from two to four pairs, most of the species with three pairs, these the posterior ones in each case, all simple tubular, with somewhat enlarged atrium, all much smaller than the thoracic; derm pores showing some variation, although all of the multilocular disk type, some with single center and about six loculi, some with more loculi, and the centers perhaps bilocular, trilocular, or quadrilocular, some larger with large unmodified center, producing straight glassy threads, some large and single with trilocular center and protruding central tongue, none of these types very heavily chitinized; derm without spines, but with setae, varying much in abundance, size, stoutness, color, and arrangement and with hairs, these usually slender with swollen bases, few in number in most species, but numerous in one genus; anal tube short, with simple ring at inner end, excepting only in Gueriniella, this retaining a double band of polygonal wax pores at inner end; ventral cicatrices one to seven in number, placed in a transverse row across abdomen behind genital opening and beneath anal opening.

Preadult females.—Where known, in general resembling the adult rather closely.

Larva.—Elliptical in outline; derm membranous; antennae six-segmented, at least moderately slender, bearing some long to very long setae and distinctly differentiated, stouter, sensory setae; legs moderately slender to slender, not otherwise unusual, the claw usually with one denticle, the claw digitules usually surpassing claw apex and slightly knobbed at tips; beak short conical, one-segmented or rather indistinctly two-segmented, the apical sensory setae truncate at apices, usually expanded and sometimes slightly bifid; thoracic spiracles large, with bar, sometimes with a single pore adjacent to opening; abdominal spiracles much smaller, simple, with somewhat enlarged atrium, constricted within to a narrow tube, in not more than four pairs, rarely in two pairs, usually in three pairs, these in each case always the posterior ones; derm pores of a simple multilocular disk type, mostly with few loculi, the arrangement of the central area varying somewhat, most frequently trilocular or triangular, these pores arranged in longitudinal rows dorsally and ventrally, in addition with a circle of disk pores around anal opening; derm without spines; derm setae present in rows, fairly abundant, often conspicuously elongated or enlarged, the apex of the abdomen usually with two or three pairs much elongated, the margin of the body sometimes with much elongated setae as well; derm hairs present but apparently always few and small, probably confined to the ventral surface, usually with enlarged, almost hemispherical bases: anal tube developed, always with a double band of polygonal

wax pores at inner end and with a circle of multilocular disk pores around opening; ventral cicatrices represented by a single circular median one.

Adult male.—Of the usual elongate shape; apex of head triangular in outline, bearing disk pores and setae, and small, usually hemispherical, tubercles beneath; antennae 10-segmented, the segments beyond the second each binodose and with two whorls of long setae, the apical segment approximately equal in length to the preapical; wings dark in color, mostly rather shorter and broader than with the other groups, the diagonal vein extending only about as far as the midpoint of a line produced along the vein to the wing margin; legs slender, the anterior femora with some, probably usually with many, bifurcate setae, claw slender, curved, denticles extending a little more than half way to claw apex; halteres flattened, with a few (perhaps three or four) curved apical setae; abdomen membranous, usually with some more heavily chitinized darker markings, with only a single apical pair of fleshy tassels, these long or short; penis sheath broader at base, more or less elongate, tapering nearly uniformly or slightly constricted toward apex, the fleshy penis bearing numerous spinelike hairs; apex of abdomen with two or three pairs of very distinctly developed spiracles, the number corresponding to that found in other stages; derm pores of a single general type, this quadrilocular disk, but the number of loculi rarely ranging from three to five; derm bearing slender setae only, these varying much in size, largest at apices of tassels.

The tribe Iceryini, as here constituted, is widely distributed. The apparently natural occurrence of its representatives includes certainly the western half of the Palaearctic region, all of the Ethiopian region, the Indian and Indo-Malayan subregions and possibly the other subregions of the Oriental region, the Australian and Austro-Malayan subregions of the Australasian region, all of the Neotropical region, and the lower portion of the Rocky Mountain subregion, and perhaps of the Alleghenian subregion of the Nearctic region, although this last is probably not an expression of true natural distribution.

The indications from published literature are that the species included in the tribe usually have a life cycle with one generation annually, but that some may shorten the period to an extent that may permit as many as three generations annually. There is no evidence at present that the cycle may ever be extended so that more than a year is required for its completion.

The genera included here fall into two very distinct groups, one including the single genus Gueriniella, the other the remaining four genera, Auloicerya, Crypticerya, Icerya, and Steatococcus. The differences are so pronounced that there is some basis for considering the two groups as distinct tribes, but no such separation is attempted here, as the evidence is not sufficiently complete. As an example of this lack of evidence, males of Gueriniella, Crypticerya, and Steatococcus are not known at all. The genera assigned to the tribe may be differentiated by the following keys:

Keys to Genera of Iceryini

ADULT FEMALE

a. Beak long conical, three-segmented, the basal very narrow; with four pairs of abdominal spiracles; derm hairs fairly abundant over both surfaces of body; anal tube retaining a band, two pores wide, of polygonal wax pores at inner end; ovipositing in a loose mass of cottony secretion (Group 1)---------- Gueriniella

aa. Beak short conical, at most indistinctly two-segmented; with not more than three pairs of abdominal spiracles; derm hairs few, apparently confined to ventral surface; anal tube with a simple chitinized ring at inner end; oviposition habit otherwise (Group 2).

b. Forming a definite internal marsupium at maturity, this communicating with the exterior through a relatively small midventral opening ..... Steatococcus

bb. Not forming an internal marsupium, reproductive habit otherwise.

c. Ventral surface of abdomen with a definitely developed band of pores, the ovisac band, most conspicuous across the abdomen behind posterior legs, this secreting an ovisac, varying in size from a flattened pad covering the venter of the abdomen to an elongate sac sometimes more than twice the length of the body ..... Icerya

cc. Ventral surface of abdomen without definite ovisac band of pores, no ovisac formed.

d. Derm remaining membranous, or nearly so; oviposition, so far as known, taking place directly beneath the body of the insect, this becoming increasingly concave ventrally ..... Crypticerya

dd. Derm becoming fairly heavily to heavily chitinized at maturity; body tending to form a longitudinal groove beneath for the reception of the eggs. (The larval characters separating this and the preceding are much more pronounced) ..... Auloicerya

LARVA

a. With four pairs of relatively conspicuous abdominal spiracles. (Group 1.) Gueriniella

aa. With not more than three pairs of abdominal spiracles, these often inconspicuous. (Group 2.)

b. Dorsal and lateral marginal setae much enlarged, stout, tips not acute. Auloicerya

bb. Dorsal and lateral marginal setae, while sometimes very elongate, not stout, tapering to very slender delicate tips. (The larvae of the three remaining genera are incompletely known nd the available information regarding them is contradictory; there appears to be no definite basis for separating the larval stages of these three genera.)

Crypticerya
Icerya
Steatococcus

ADULT MALE

Adult males are known certainly for only two of these genera, Icerya and Auloicerya. There seems to be little difference between the two. The penis sheath in the latter is more elongate and more nearly linear than in species of Icerya, which may be of possible generic significance.

GROUP 1

Genus Gueriniella Fernald

(Pl. 7, B, and figs. 105 and 106)

This genus was first established as a zoological unit by Targioni-Tozzetti (*162, p. 724*) in 1869, at which time the name Guerinia was utilized for its designation, and a single species, *Coccus serratulae* Fabricius (*44, p. 744*), which thus becomes the genotype, was included. No other species has been added to the genus subsequently. Investigation of literature at the time of publication of the Fernald catalogue (*46, p. 331*) showed that this generic name had been used previously in the insect order Diptera and the name Gueriniella was therefore substituted.

As there seems to be no present-day ambiguity as to the actual species of insect to be associated with this generic name and the species name *serratulae*, the writer has refrained from an exhaustive study of the early literature referring to this insect.

GENERIC CHARACTERISTICS

Habit.—Living on the stems of the host, protected only by secreted matter; producing a conspicuous mass of white cottony secretion at time of oviposition, this surrounding both the insect and the eggs.

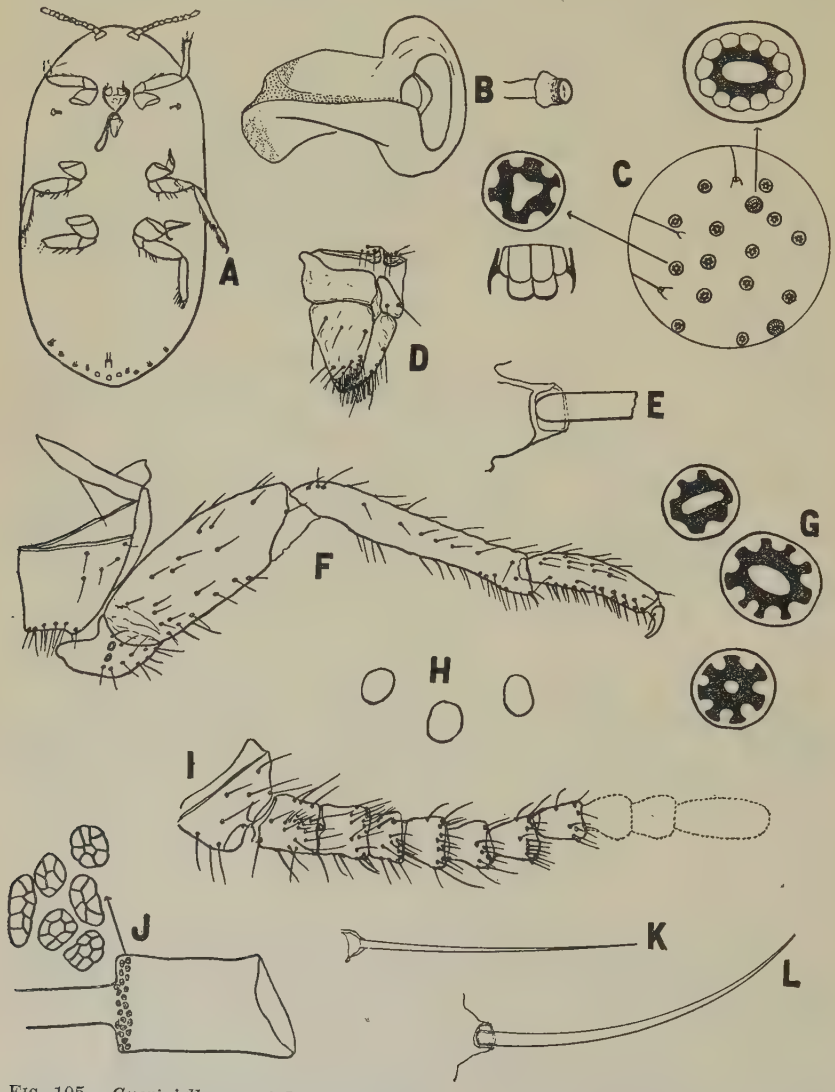

FIG. 105.—*Gueriniella serratulae*, adult female: A, outline, optical section, × 7.5; B, thoracic and abdominal spiracles, × 165; C, section of dorsal derm, × 230, with details of pores, × 1,500; D, beak, × 60; E, base of largest type marginal seta, × 650; F, leg, × 60; G, derm disk pores, × 1,500; H, ventral cicatrices, × 50; I, antenna, × 60; J, anal tube, × 115, with detail of polygonal wax pores, × 650; K, body hair, × 650; L, body seta, × 650

Adult female.—Body elliptical in shape; the derm remaining membranous at maturity; antennae 11-segmented, of the normal iceryine type; legs well developed, lower tibial and tarsal setae almost spinelike, claw large, without denticle, digitules pointed or at least slender at tips, nearly reaching claw apex; beak relatively long conical, evidently three-segmented, the basal very narrow.

apex with blunt-tipped but not expanded sensory setae; rostral filaments rather short, the loop hardly reaching the second coxae, much as in Icerya; thoracic spiracles large, with bar, not accompanied by pores; with four posterior pairs of simple, short tubular, abdominal spiracles; derm pores of a single type, but of more than one sort, a few ventrally with oval center and about 10 to 11 loculi but most of pores with triangular or elongate center and 6 loculi; derm setae present, scattered, slender, mostly rather small, some, along body margin, much more conspicuous, with definite stout conical basal collars; hairs present, slender, similar to those of Icerya, with conical or rounded bases, fairly numerous on both surfaces; anal opening surrounded by a circle of disk pores, the inner end of the anal tube with a band of polygonal wax pores; ventral cicatrices from three to five with the outer two, if present, much smaller than the others.

Larva.—Body elliptical; antennae six-segmented, the apical much larger, of normal iceryine type; legs of normal type, digitules slightly enlarged at tips, exceeding claw, this with a small denticle near apex; beak short triangular, apparently only two-segmented, the basal segment very narrow and indistinctly separated from the larger apical; thoracic spiracles with stout bar; abdominal

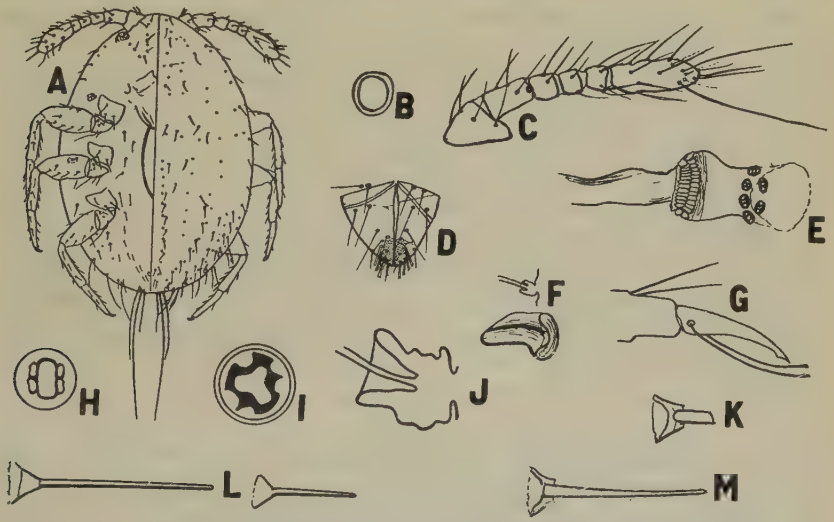

FIG. 106.—*Gueriniella serratulae*, larva: A, outline, dorsal and ventral, × 60; B, ventral cicatrix, × 330; C, antenna, × 115; D, beak, × 115; E, anal tube, × 330; F, abdominal and thoracic spiracles, × 115; G, claw, × 530; H, ventral derm pore, × 1,500; I, dorsal derm pore, × 1,500; J, abdominal spiracle, × 1,500; K, base of apical seta, × 650; L, dorsal hairs, × 650; M, submarginal seta, × 650

relatively large, short tubular; derm pores of one type, but with centers varying from triangular to elongate, as in adult; derm setae in definite rows, stouter and larger toward margin, with definite conical bases; a few hairs present, with expanded bases as with Icerya; marginal setae not conspicuously larger than dorsal, the apical setae in two sets of three, with the middle seta of each set conspicuously longer and larger than the other two, these only somewhat larger than the lateral marginal setae; anal opening with a disk pore collar, inner end of tube with a double band of polygonal wax pores; with a single, median, ventral cicatrix.

Adult male.—Not known.

The single included species is known from western Europe and adjacent portions of the North African coast.

The writer has met with no definite information regarding the life history of this insect.[33] According to information received

[33] This has been discussed very recently and in great detail by Vayssière (*170, p. 222–256*). According to him, in France at least, there is one generation annually, with growth from larva to adult female from early spring to summer, egg laying and hatching in midsummer, and an extended quiescent larval period till the following early spring.

from Algeria, from Mr. Balachowsky, the female appears in the spring. This suggests an annual cycle, probably with an extended egg stage and rapid growth coinciding with the period of most active growth in the plant.

GROUP 2

Genus Crypticerya Cockerell

(Pl. 7, C, and figs. 107 and 108)

This genus was established by Cockerell (*9, p. 15*) in 1894 to include the single species *Icerya rosae* of Riley and Howard (*155*). The chief basis given for the segregation was the absence of an ovisac at maturity in the adult female.

GENERIC CHARACTERISTICS

Habit.—Living freely exposed on the leaves and branches of the host, sometimes protected by ant cartons; eggs placed directly beneath body, which becomes more and more concave beneath as they are deposited.

Adult female.—Secretionary covering varying from partial to heavy, with protruding portions; shape of body varying from slightly ovoid to elliptical, from slightly to very strongly convex, but in all cases more or less distinctly concave beneath; derm remaining membranous, or becoming very slightly chitinized at maturity; antennae 9-segmented to 11-segmented, of the same general type as in Icerya; legs resembling those of Icerya; beak short conical, but with a very faint indication of a joint near base in some species; thoracic spiracles with bar; abdominal spiracles in three pairs, these simple and posterior; derm pores of one or more types, ordinary multilocular disk, open center beaded, or large trilocular center with beaded rim; derm setae as in Icerya, with definitely formed collars, these setae in general rather abundant and widely distributed and the body margin with clusters of much longer and larger setae than those on the dorsum or venter; hairs with rounded bases present; anal tube with a simple ring at inner end; normally with three ventral cicatrices, sometimes with only one.

Preadult female.—Where known, in general resembling the adult rather closely.

Larva.—Body elongate-elliptical to elliptical; antennae six-segmented, with long setae, slender except in one species; legs as in Icerya; beak very short conical, one-segmented, with blunt-tipped, apical, sensory setae; thoracic spiracles with bar; abdominal spiracles simple tubular, minute, in the three posterior pairs; derm pores of a single multilocular disk type, arranged in apparent longitudinal rows; derm setae slender, but relatively elongate in comparison with larvae of other genera in the group, both the apical and marginal setae very long and conspicuous, although with the three pairs of apical setae distinctly longer than the lateral marginal ones; anal tube with the usual internal band of polygonal wax pores, and with a ring of disk pores at the opening; with a single median ventral cicatrix.

Adult male.—Not certainly known.

The positively known distribution of this genus, as here accepted, includes the three upper subregions of the Neotropical region, the three continental subregions of the Ethiopian region, and the Indo-Malayan subregion of the Oriental region. The occurrence of the genotype at Key West, Fla., is considered as probably due to introduction by man. As indicated below, the different species found in the three major regions of distribution outlined are considered to represent definite groups, which, while not so indicated here, may possibly deserve at least subgeneric standing.

There seems to be no definite information available regarding the detailed life cycle of any of the species included here; probably there is a single generation annually in those areas in which the seasonal

changes are more pronounced, with more or less doubling up of the generations in tropical and subtropical regions.

The groups of species that have been recognized within this genus may be separated by the following keys:

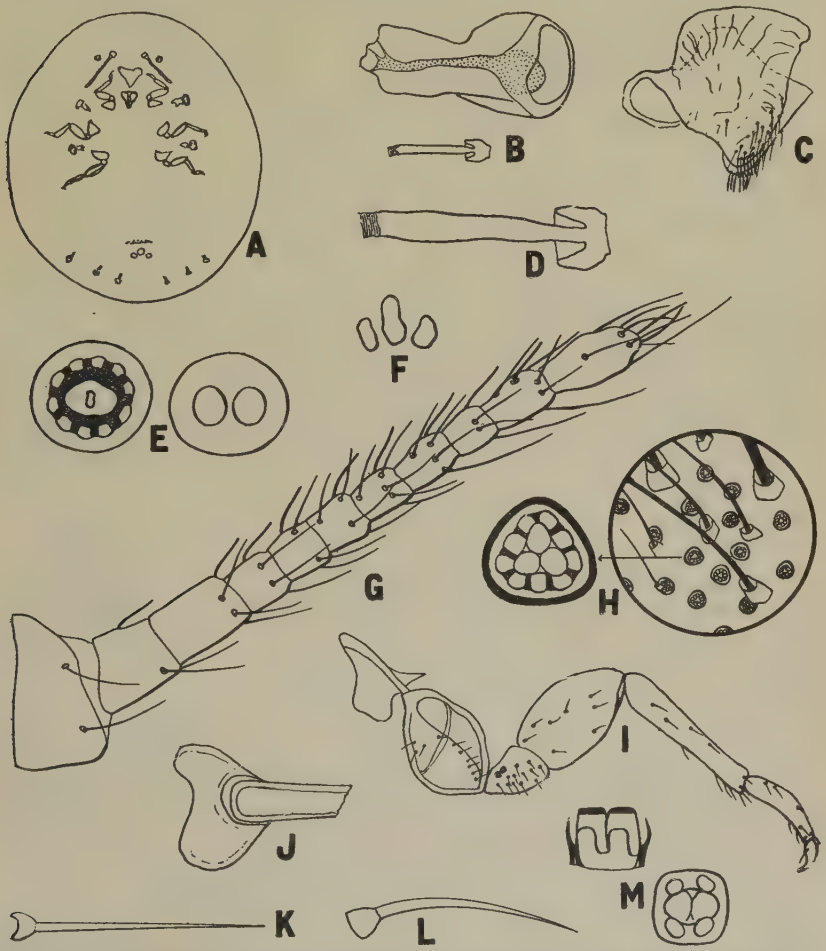

FIG. 107.—*Crypticerya rosae*, adult female: A, outline, optical section, diagrammatic, × 10; B, thoracic and abdominal spiracles, × 230; C, beak, × 60; D, abdominal spiracle, × 650; E, derm disk pore, two views, × 1,500; F, ventral cicatrices, × 30; G, antenna, × 115; H, section of derm, × 230, with detail of pore, × 1,500; I, leg, × 56; J, base of largest type marginal seta, × 650; K, average ventral hair, × 650; L, average dorsal hair, × 650; M, derm disk pore, surface and section, × 1,500

KEYS TO GROUPS OF SPECIES OF CRYPTICERYA

Adult female

a. Derm without specialized multilocular disk pores, one sort only present, this ordinary multilocular disk, with circular, triangular, oval, or elongate centers; body somewhat ovoid in shape, broader behind, strongly convex above.....Group 1 (Neotropical)

aa. Derm with specialized disk pores of some sort; body more nearly elliptical, much less strongly convex.

b. Body with numerous disk pores with trilocular centers and protruding tongue in clusters along margin, these producing unusually long, fingerlike wax processes.....Group 2 (Oriental)

bb. Body with large disk pores with clear central area each with deep cup, arranged in marginal clusters; without trilocular center pores or fingerlike wax secretion----------Group 3 (Ethiopian)

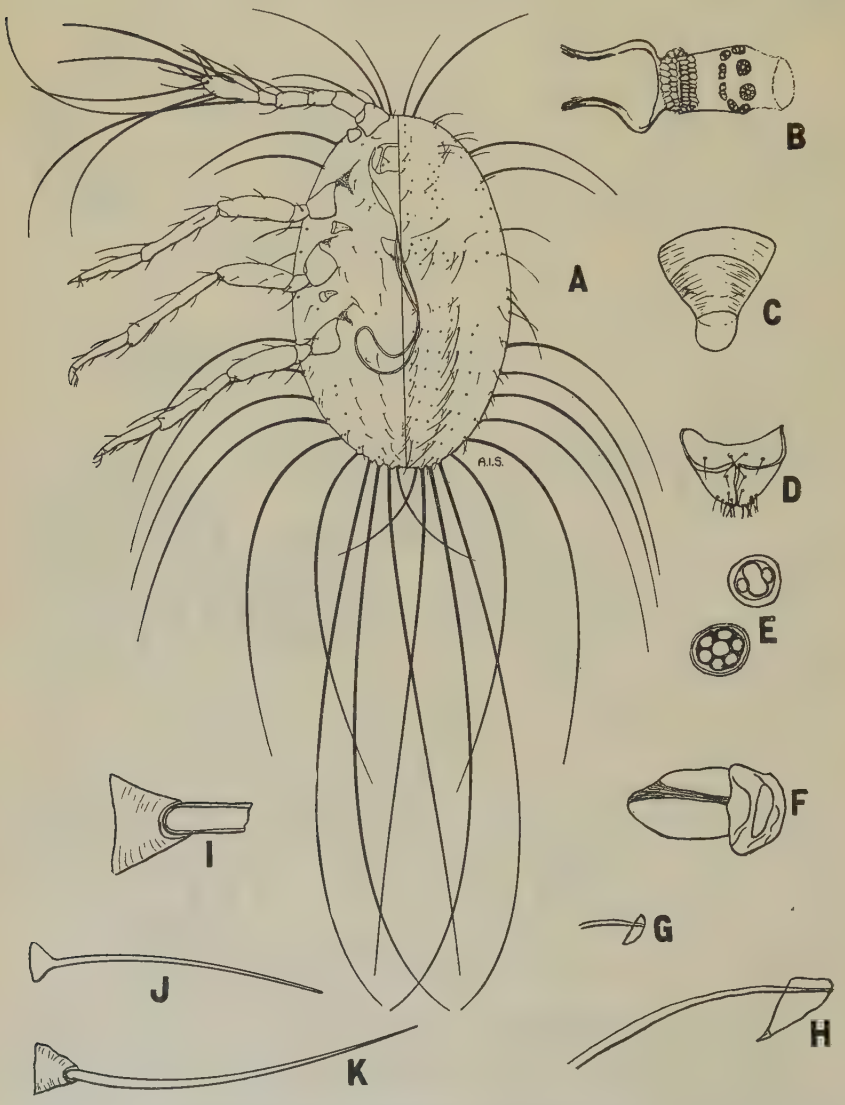

FIG. 108.—*Crypticerya rosae,* larva: A, outline, dorsal and ventral, × 60; B, anal tube, × 330; C, ventral cicatrix, × 330; D, beak, × 115; E, derm pores, × 1,280; F, thoracic spiracle, × 460; G, abdominal spiracle, × 460; H, abdominal spiracle, × 1,280; I, base of marginal seta, × 650; J, body hair, × 650; K, dorsal body seta, × 650

Larva

a. With three pairs of apical setae.
b. Lateral marginal setae not each accompanied by an additional seta nearly as long as itself----------Group 1 (Neotropical)
bb. Lateral marginal setae each accompanied by an additional seta nearly as long as itself----------Group 2 (Oriental)
aa. With only two pairs of apical setae----------Group 3 (Ethiopian)

A number of species have been given consideration with reference to their possible inclusion in this genus. Of these, the species enumerated below are regarded as fairly definitely assignable to it. Group 1 (Neotropical): *abrahami* Newstead (*151, p. 1*) from British Guiana; *primitiva* variety *pimentae* Newstead (*151, p. 2*) from Jamaica; *rosae* Riley and Howard (*155, 156*) from Key West, Fla.; Group 2 (Oriental): *jacobsoni* Green (*68, p. 316*) from Java; Group 3 (Ethiopian): *ewarti* Newstead (*140, p. 132*) from West Africa (placed from description only); and *natalensis* Douglas (*38, p. 86*) from South Africa.

Besides these, it seems quite possible that *bicolor* Newstead (*151, p. 7*),[34] *cajani* Newstead (*151, p. 6*),[34] and *caudatus* Newstead (*151, p. 6*)[35] may also belong here, but no specimens have been available for a verification of this tentative opinion.

The series of specimens studied is too incomplete to permit an attempt to separate by keys even the few species definitely included here. From the American specimens examined, it seems quite possible that ultimately, when the several stages and the life cycles of specimens from a number of different localities are well known, a group of closely related species will be recognized, thus paralleling the condition already known to exist in some other genera, such as Drosicha.

Genus Icerya Signoret

(Pl. 7, D, and figs. 109, 110, and 111)

This genus was first erected by Signoret (*158, p. 357*) in 1875, with the single included species *Coccus sacchari* Guérin (*82, p. 451*), which consequently stands as the type. This species was subsequently accepted as being synonymous with *Dorthezia seychellarum* Westwood (*173*), and this last name is that usually referred to when the genotype is mentioned. The notorious cottony cushion scale was added to the genus shortly after its erection, and subsequently other additions have been made, until the present total number of species, subspecies, and varieties that have been assigned here, some of which are now regarded as synonymous, far surpasses that included in any other genus in the subfamily.

A few generic synonyms of Icerya have been created. Crossotosoma was used by Douglas (*39, p. 79*) in 1890 for the species now called *Icerya aegyptiaca*. Cockerell (*9, p. 15*) in 1895 erected the subgenus Proticerya, with *I. rileyi* as type, but this is not at present accepted as valid. MacGillivray (*119, p. 71*) in 1921 established a genus, Newsteadiella, on a misinterpretation of the description of *Icerya formicarum* Newstead.

GENERIC CHARACTERISTICS

Habit.—Living exposed on the leaves and branches of the host during the growing period; producing a definitely formed ovisac, sometimes only a pad of secretion beneath the body of the adult female, usually protruding somewhat behind the body to as much as twice its length.

Adult female.—Body externally more or less completely covered with rather waxy secretion, this tending, where well developed, to take on the form of

[34] According to Vayssière (*170, p. 315*), who examined specimens. these two species actually do belong in this genus.

[35] According to Vayssière (*170, p. 307*), who examined specimens, this should be assigned to the genus Steatococcus.

plates or tufts, margins of body with definite waxy plates or tufts more or less developed; body elliptical to ovoid, if the last, then broadened behind; derm remaining membranous and colorless at maturity; antennae of the normal monophlebine type, 9-segmented to 11-segmented; legs of the normal monophlebine type, claw without a denticle, claw digitules acute at apices, not exceeding the claw tip; beak very short and stout conical, one-segmented, with

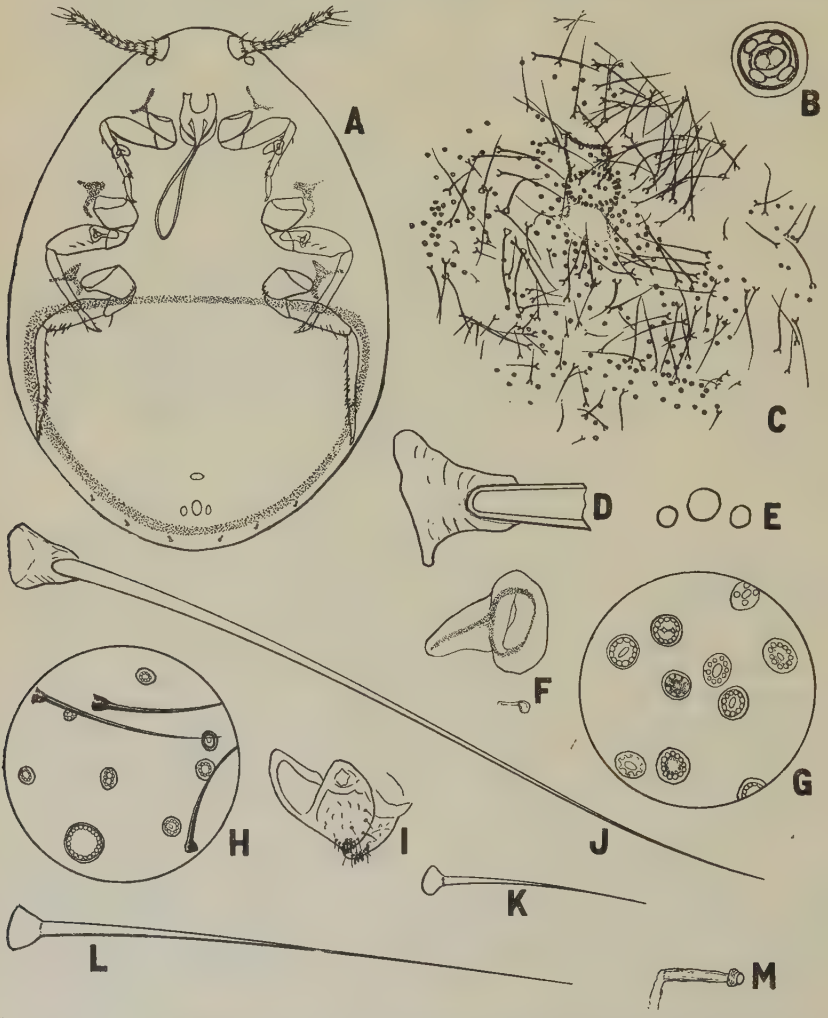

FIG. 109.—*Icerya seychellarum*, adult female: A, outline, ventral, × 12; B, dorsal derm pore, × 1,280; C, anal region, × 60; D, base of largest type marginal seta, × 650; E, ventral cicatrices, × 30; F, thoracic and abdominal spiracles, × 60; G, section of anterior portion of ovisac band, × 530; H, section of middorsal derm, × 220; I, beak, × 60; J, dorsal seta, × 650; K, ventral hair, × 650; L, dorsal hair, × 650; M, abdominal spiracle, × 120

broadened, blunt-tipped, or even bifid sensory setae; with two or three pairs of small, simple, posterior abdominal spiracles in addition to the usual two pairs of much larger thoracic spiracles, these last each with bar but without disk pores at opening; derm pores showing much variation in details of organization, but of two general types, the one large, with open center and a marginal band of loculi, the other smaller, and variable in size, with a marginal band of loculi, but with bilocular, trilocular, or quadrilocular or other modification

of the center; derm setae usually slender, rather hairlike but stout and spinelike in a few species, abundant and closely crowded or very sparse, with definite truncate conical basal collars; hairs present, few in number, with hemispherical to flat conical bases; pores grouped in the ventral abdominal region to form a definite ovisac-secreting band, through which may usually be found a number of hairs, these occurring in varying numbers and sizes from rare to very

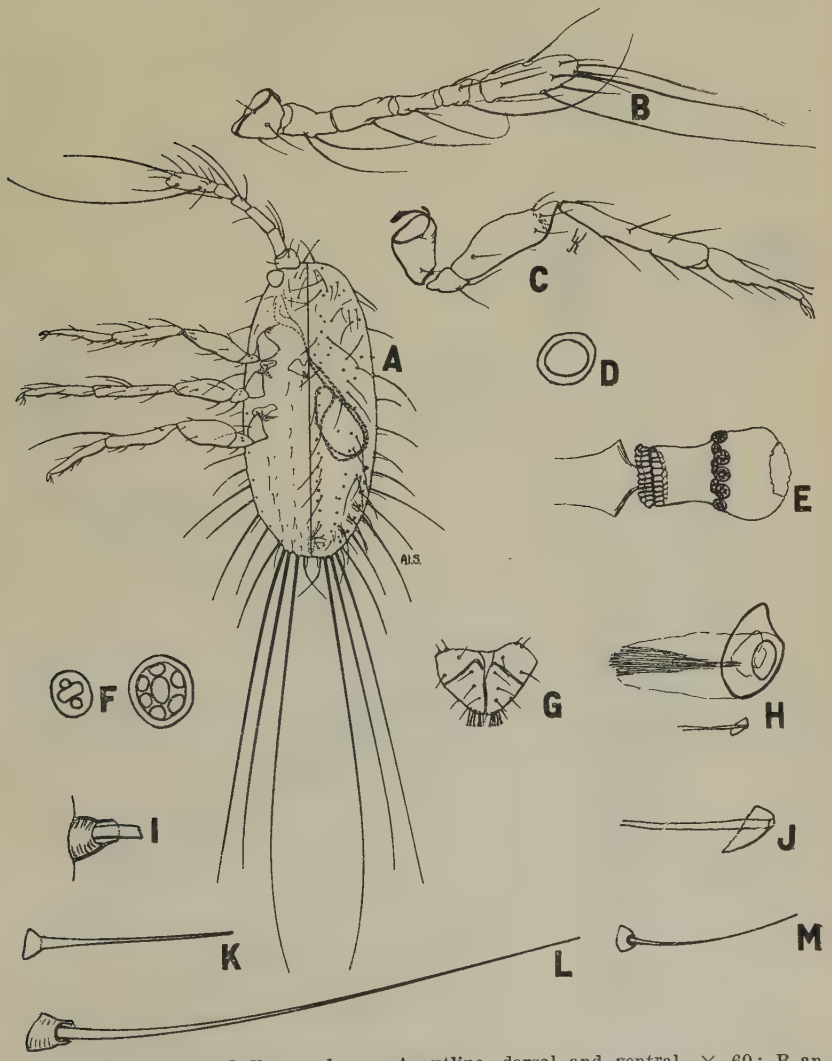

FIG. 110.—*Icerya scychellarum*, larva: A, outline, dorsal and ventral, × 60; B, antenna, × 115; C, leg, × 115; D, ventral cicatrix, × 330; E, anal tube, × 330; F, derm pores, × 1,280; G, beak, × 115; H, thoracic and abdominal spiracles, × 460; I, base of apical seta, × 650; J, abdominal spiracle, × 1,280; K, dorsal hair, × 650; L, dorsal seta, × 650; M, ventral seta, × 650

numerous and from small to large, this ovisac band transverse and most obvious immediately behind the posterior coxae; anal tube membranous with a simple, relatively large, circular ring at inner end; ventral cicatrices ranging in number from one to seven, the usual number three, all in a transverse row across the venter of the abdomen immediately behind the genital opening, this row often curved toward the apices.

Preadult female.—In general closely resembling the adult.

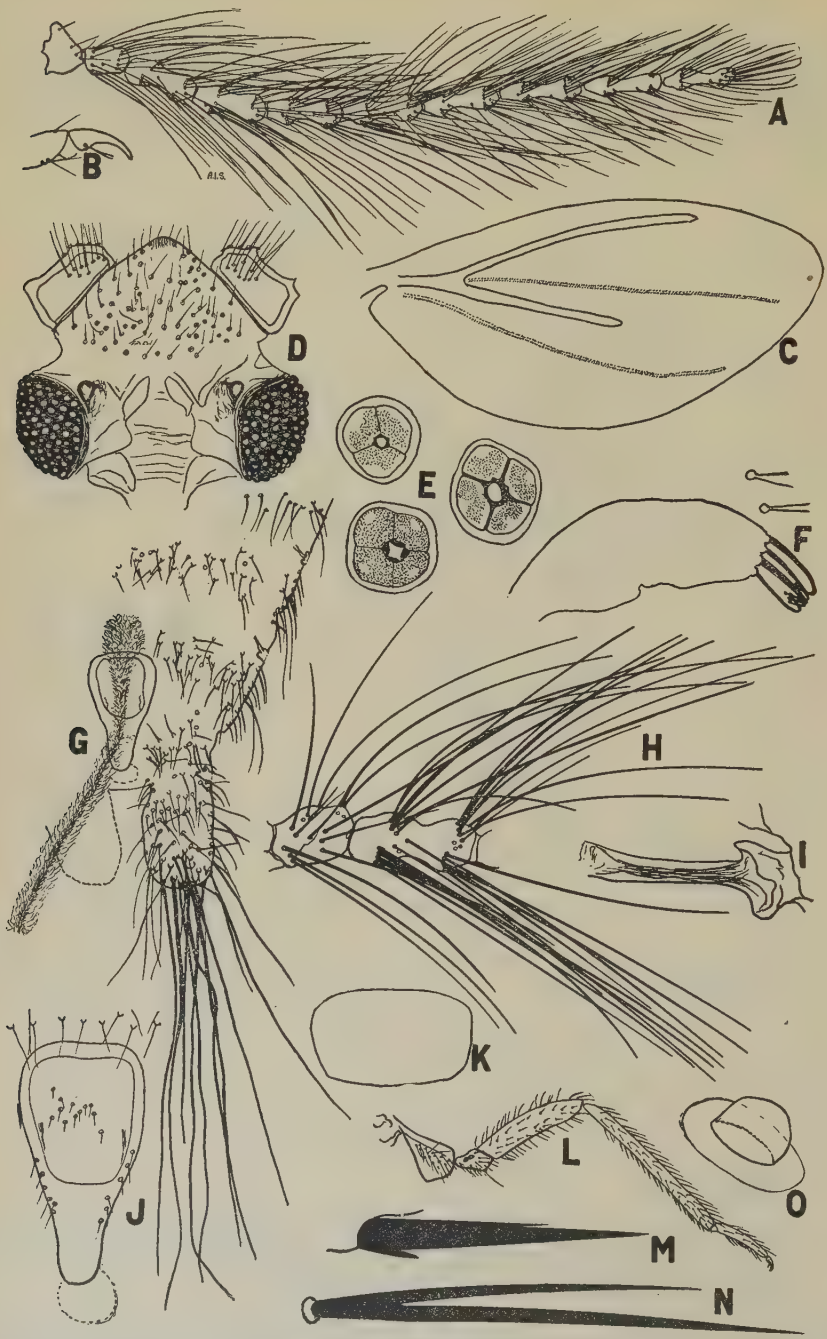

FIG. 111.—*Icerya seychellarum*, adult male: A, antenna, × 30; B, claw, × 120; C, wing, × 17.5; D, head, × 60; E, abdominal derm disk pores, × 1,280; F, halter, × 230, with detail of seta tips, × 650; G, apex of abdomen, × 60; H, second and third antennal segments, × 60; I, abdominal spiracle, × 530; J, penis sheath, × 120; K, outline of oblong, unchitinized, middorsal thoracic area, × 230; L, leg, × 30; M and N, bifurcate setae from leg, × 230; O, tubercle from head, × 1,280

Larva.—Body broad elliptical; antennae six-segmented, the apical segment strongly enlarged and bearing several long to very long setae; legs normal, mostly relatively long and rather slender, claw slender, with denticle, claw digitules extending beyond claw apex, slightly swollen or knobbed at tips; beak very short and stout conical, one-segmented, with subapical group of blunt-tipped or bifid setae; thoracic and abdominal spiracles, in general, as in adult, that is, the thoracic with a bar, without pores, the abdominal simple, in two or three pairs; derm pores of a single type only, small multilocular disk; body setae of one general type, mostly slender, basal collar stout conical; hairs with approximately hemispherical bases present; marginal setae definitely differentiated, the apical setae, at the apex of the abdomen, in three or sometimes in two pairs, if the last, due to reduction of the median pair of the three, the lateral setae along the body margin anterior to the apical distinctly differentiated in size from these, each of these laterals sometimes accompanied by a second seta of considerable size; anal tube short, with a ring of polygonal wax pores at its inner end, a ring of disk pores somewhat beyond these, and a more or less distinct circle of disk pores around or near its external opening; with a single circular, median, ventral cicatrix.

Adult male.—Of the usual elongate shape; head triangular in outline apically; antennae 10-segmented, all beyond the second binodose and each with two whorls of setae; wings dark, the basal diagonal vein hardly reaching half way to the margin; legs normal, slender, anterior femora with bifurcate setae, tarsus two-segmented, claw without denticle, claw digitules hairlike, tapering, not attaining claw apex; only the apical pair of abdominal fleshy tassels present; penis sheath relatively stout and short, slightly contracted before apex; disk pores of the usual type, number of loculi varying from a normal of four; abdominal spiracles as in other stages, that is, two or three pairs.

This is, on the basis of our present knowledge, the most widely distributed genus in the whole subfamily. Presumably indigenous species have been reported from the Mediterranean subregion of the Palaearctic region (very possibly not truly indigenous); from the East African and West African subregions of the Ethiopian region; from the Indian (including Ceylon) and the Indo-Malayan subregions of the Oriental region; from the Australian subregion of the Australasian region; from all four divisions of the Neotropical region, and from the Rocky Mountain subregion of the Nearctic region. The records indicate a circumequatorial distribution for the genus, with probable complete exclusion from natural occurrence in the Palaearctic region and very limited occurrence in the Nearctic and Australian regions. Quantitatively the Neotropical region appears to be the present center of natural distribution.

Some careful and fairly extended work has recently been carried out on the annual cycle of at least one included species, *Icerya purchasi*, by Kuwana (*108, p. 12*); with this, under presumably optimum conditions, three generations may be obtained annually. Probably this species under less favorable circumstances, as well as most of the other species assigned here, agrees with the genotype in having one generation annually, a fact shown in this same paper.

Although specimens of type or other authentic material of well over half of the included species and varieties have been available for study, it has not proved practicable to form really satisfactory groups among these species, and definite segregation of this kind must await the collection of additional material, and particularly of additional stages of species now inadequately represented.

From a study of specimens and literature, the following species have been retained in the genus, each having been described as or being currently accepted as belonging to Icerya unless otherwise indicated: *aegyptiaca* (Douglas) (*39, p. 79*), *albolutea* Cockerell (*13*), *brasiliensis* Hempel (*91, p. 370*), *chilensis* Hempel (*95, p. 333, 357*),

colimensis Cockerell (*22, p. 81*), *corticalis* Vayssière (*170, p. 321*), *flava* Hempel (*95, p. 334, 358*), *formicarum* Newstead (*141, p. 169*), *genistae* Hempel (*92, p. 18, 55*), *koebelei* Maskell (*125, p. 184*), *littoralis* Cockerell (*14, p. 429*) and varieties *mimosae* Cockerell (*14, p. 430*) and *tonilensis* Cockerell (*22, p. 81*), *longisetosa* Newstead (*148, p. 155*), *luederwaldti* Hempel (*93, p. 197*), *maxima* Newstead (*150, p. 301*), *maynei* Vayssière (*170, p. 326*), *minima* Morrison (*132, p. 64*), *minor* Green (*66, p. 17*), *montserratensis* Riley and Howard (*156, p. 99, 101*), *nigroareolata* Newstead (*151, p. 8*), *palmeri* Riley and Howard (*156, p. 104*), *pilosa* Green (*64, p. 7*), *pulcher* (Leonardi) (*111, p. 3*) (described as Palaeococcus), *purchasi* Maskell (*121, p. 221*) and varieties *citriperda* Hempel (*94, p. 112; 95 p. 331, 361*), *crawii* Cockerell (*11*), and *maskelli* Cockerell (*11*), *rileyi* Cockerell (*9, p. 15*) and variety *larreae* Cockerell (*22, p. 82*), *schrottkyi* Hempel (*91, p. 373*), *schoutedeni* Vayssière (*170, p. 337*), *seychellarum* (Westwood) (*173*) and varieties *cristata* Newstead (*146, p. 11*) and *nardi* Green (*65, p. 441*), *splendida* Lindinger (*114, p. 85*), *subandina* Leonardi (*112, p. 238*), *sulfurea* Lindinger (*114, p. 85*) and variety *pattersoni* Newstead (*151, p. 9*), *tremae* Vayssière (*170, p. 344*), and *zeteki* Cockerell (*31*).

Of the other species that have been described as Icerya and are currently assigned to this genus, the following have been excluded: *euphorbiae* Brain (*3, p. 167*) (=Steatococcus), *hyperici* Froggatt (*55, p. 472*) (status not certain from the description), *insulans* Hempel (*96, p. 510*) (status not certain from description), *jacobsoni* Green (*68, p. 316*) (considered to represent a species of Crypticerya), *natalensis* Douglas (*38, p. 86*) (=a species of Crypticerya), *paulista* Hempel (*95, p. 336, 360*) (status not certain from description), *taunayi* Hempel (*95, p. 340, 364*) (status not certain from description).

Some comparatively recently described species have been placed in synonymy, these including three, *candida* Cockerell (*27, p. 128*), *crocea* Green (*64, p. 7*), and *okadae* Kuwana (*104, p. 178*) as synonyms of *seychellarum* (Westwood), and *tangalla* Green (*64, p. 7*) as a synonym of *aegyptiaca* (Douglas).

The key that follows includes only those forms for which specimens of the stage keyed have been available for study, is fragmentary in other respects, is distinctly not based on a thorough and critical study of the species involved, and at most will probably only serve to indicate tentatively some of the groups of species to be found within the genus.

KEY TO AVAILABLE SPECIES OF ICERYA

Adult female

a. With two pairs of abdominal spiracles.

b. Derm setae conspicuously blackish, hairlike, mostly grouped in obvious clusters; lateral ventral cicatrices approximately circular in shape, distinctly smaller than the median; secreting a distinct and conspicuous ribbed posterior ovisac; dorsum mostly only thinly covered with secretion.

c. Antennae normally 10-segmented; body, even at maturity, with a dorsal cylindrical pencil of secreted wax ..... *koebelei* Maskell [36]

[36] See Morrison and Morrison (*138, p. 33*) for some discussion of this species. The writer considers it possible that the species may be based on an abnormal colony of *I. purchasi* Maskell, although Froggatt (*55, p. 471*) reports finding it (rarely) about Sydney, New South Wales.

cc. Antennae normally 11-segmented; body without middorsal pencil of secretion ..... *purchasi* Maskell
including var. *crawii* Cockerell [37] and *maskelli* Cockerell

bb. Derm setae not blackish, less hairlike, and, while grouped, not forming conspicuous tufts; lateral ventral cicatrices elliptical or kidney-shaped, approximating the median in size; body concealed beneath a large loose mass of white secretion, the ovisac not differentiated from this.
callitri (Froggatt)

aa. With three pairs of abdominal spiracles.

d. Derm dorsally, in addition to the usual types, with large, conspicuous "open-center" or "beaded-rim" pores, arranged in small clusters or in transverse rows.

e. Large "open-center" pores, very conspicuous, owing to small size of body and presence of a blackish chitinized border around each, this border frequently inclosing also a seta base or a much smaller multilocular disk pore, these large pores in clusters along margin and in rows across dorsal surface on whole body; with a single, median, circular, ventral cicatrix (perhaps not constant); antennae normally nine-segmented or less.
pilosa Green [38] and *nardi* Green

ee. Large "open-center" pores much less conspicuous, owing in part to larger size of body, in part to restriction in distribution, here occurring on the middorsal portion of the posterior abdominal segments, but mostly to reduction of blackish chitinized border to a very narrow band; normally with three small, circular, ventral cicatrices; normally with 11-segmented antennae.
seychellarum (Westwood)

dd. Derm, while often showing distinct variation in pore types, without the large "open-center" or "beaded-rim" type found in the preceding.

f. Ovisac band well developed, with pores and long hairs or setae, these numerous, approaching the pores in number, at least in the anterior median section of the band; antennae normally nine-segmented but variable.

g. Body setae few in number, mostly conspicuously stout, apices of all except those around anal opening bluntly rounded; hairs in ovisac band large and stout, likewise bluntly rounded at apices ..... *minima* Morrison

gg. Body setae much more numerous and, although sometimes large, proportionately much more slender, tapering uniformly to acutely pointed tips; hairs of ovisac band likewise tapering uniformly to acute tips.

h. With a single, median, circular, ventral cicatrix (*colimensis* Cockerell is here regarded as a synonym).
palmeri Riley and Howard [39]

hh. With three circular ventral cicatrices.

i. With stout blackish setae, each with high conical basal collar, in the ovisac band; dorsal setae all stout, blackish, some rather large (includes variety *larreae* Cockerell).
rileyi Cockerell [40]

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[37] While some of the differences noted by Cockerell in describing these two varieties appear in microscopic mounts of cotype specimens of each, it has not proved possible to determine their exact status from this material in the brief period available for a study of the same. Probably critical breeding work will be required before definite conclusions can be reached.

[38] See Green (*65, p. 440–443*) for detailed discussion and elaborate illustrations of this and the following species.

[39] These two species were separated by Cockerell on the basis of differences in the stoutness of the larval antenna, particularly in the width of the fourth segment; measurements made recently on cotype larvae of both species give identical results, 25μ, for the maximum width of the fourth segment instead of 21μ for *colimensis* and 30μ for *palmeri* as given by Cockerell. The larvae appear to be identical in all other respects as well. Mounted adult females likewise appear to show no tangible differences, although the available material is limited and not altogether satisfactory.

[40] On the basis of the material available for study, including type lots of both species and variety, the differences in the larval antennae, cited by Cockerell as a basis for separating the two, are nonexistent; the antennae of both are of about equal stoutness and the second segment is slightly longer than the third in both. No obvious distinguishing characters appear in the adult female, although the setae in the variety, including those in the ovisac band, appear to be somewhat less stout and somewhat lighter in color than in the type, but no other differences have been noted in the limited material of the two that has been examined.

ii. Setae in ovisac band few, slender, this mostly with slender, light-colored hairs having flat conical to nearly hemispherical bases; dorsal setae slender, not dark colored, not especially conspicuous_____*littoralis* Cockerell [41] and varieties *mimosae* Cockerell and *tonilensis* Cockerell

ff. Ovisac band often rather narrow, not particularly well developed, anterior median section without hairs or setae, or, if present there, these relatively few, inconspicuous; antennae normally 10-segmented to 11-segmented, but variable.

j. Dorsal and marginal setae very sparse, short and stout at bases, blackish, many almost spinelike; derm pores in ovisac band and elsewhere, except in genital region, small, simple multilocular disks with large, usually indistinctly bilocular or trilocular center and from 6 to 11 loculi_____*subandina* Leonardi

jj. Dorsal and marginal setae more, and usually much more, numerous, slender, lighter in color; derm pores, in many but not all species, showing an enlarged form and special type of arrangement and shape in the loculi.

k. With a single, large, median, elliptical, central cicatrix (apparently constant in a series of specimens from several localities)_____*aegyptiaca* (Douglas)

kk. With three or more circular to elliptical ventral cicatrices (*albolutea* Cockerell uncertain, but distinguished from the preceding by the development of unusual pores).

l. Size very large, mounted specimens about 14 mm. long; dorsal surface, in addition to small, usually oval multilocular disk pores, with large circular disk pores with normally six large loculi and much smaller circular disk pores with about five loculi; ventral cicatrices three, these very large, elliptical, constricted or asymmetrical; forming only a pad of secretion beneath_____*maxima* Newstead

ll. Size much smaller, length not over 8 mm. and usually less; dorsal pore combinations not as in preceding.

m. Normally with three circular to elliptical ventral cicatrices.

n. Antennae normally 10-segmented (subject to variation); anterior median section of ovisac band very narrow, hardly more than an irregular double row of small multilocular disk pores; derm pores showing several minor variations of the ordinary multilocular disk type, but none differing conspicuously from this either in size or in internal arrangement; the three ventral cicatrices small, approximately circular *pulcher* (Leonardi) and *minor* Green [42]

nn. Antennae normally 11-segmented (subject to variation); anterior median section of ovisac band broader, mostly at least three or four pores wide; derm in most of the following species with some pores, at least, conspicuously different from the ordinary multilocular disk type and its variations, these special pores often larger and more conspicuous.

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[41] No morphological basis for separating this species and its two varieties has been discovered in either adult females or larvae; since the slight color differences on which they are based are hardly significant, it seems probable that the three are identical.

[42] Type specimens of *minor* and specimens believed to be *pulcher*, on comparison, show few even apparent differences, except that *pulcher* has a definitely larger number of small disk pores dorsally.

o. Margin of body with a practically continuous loose row of enlarged, circular disk pores having normally six to eight large marginal loculi and a large central circular disk with crenulate margin showing either about 12 or about 20 lobes, these apparently representing tiny loculi.

p. Derm adjacent to above pores with an occasional still larger pore, each with large bilocular or trilocular center and usually six rather large marginal loculi introduced between the large central lobes; large circular pores usually with eight loculi and about 12 to 15 lobes on central disk.

albolutea Cockerell

pp. Large bilocular or trilocular pores as described above wanting; large circular pores usually with six, sometimes with seven, loculi and the central disk with about 20 lobes (based on specimens determined by Newstead)___*sulfurea* Lindinger.

oo. Margin of body without such enlarged circular disk pores, and with nothing exactly comparable.

q. Dorsal derm with numerous, but not crowded, somewhat enlarged, circular disk pores having small irregular center and usually eight rather large radiating loculi; no posterior ovisac, insect forming a pad of secretion beneath body.

schrottkyi Hempel

qq. No dorsal pores of the above described sort; with a distinct ribbed or fluted posterior ovisac.

montserratensis Riley and Howard and *brasiliensis* Hempel [43]

mm. Normally with five to seven circular to elliptical ventral cicatrices.

r. With five ventral cicatrices, the outer small_____*similis* Morrison [44]

rr. With seven ventral cicatrices, the outer small_____*zeteki* Cockerell

Genus Auloicerya Morrison

(Pl. 7, E, and figs. 112, 113, and 114)

This genus was established by the writer (*138, p. 22*) in 1923 to include the genotype, *Icerya rosae* variety *australis* Maskell, and a newly described species, *A. acaciae.*

GENERIC CHARACTERISTICS

Habit.—Living exposed on the host during growth, producing a marginal fringe of secretion, and the whole venter becoming somewhat concave for the reception of the eggs at oviposition.

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[43] Cotype specimens of *brasiliensis* are larger than specimens of *montserratensis,* and the three ventral cicatrices are somewhat oval to elliptical; in *montserratensis* these are approximately circular; at present the writer is inclined to consider them as probably identical.

[44] Except for the apparently constant difference in the character of the ventral cicatrices, as indicated, the series of specimens on which this is based, from Panama, Trinidad, and Tobago, seems identical, in structural characteristics, with specimens of *zeteki* from the Canal Zone and elsewhere. Probably experimental breeding will be necessary to determine their status with certainty.

Adult female.—Elliptical; externally nearly to entirely naked above; derm dorsally and at margins becoming strongly chitinized and dark brown to blackish at maturity, but with the midventral derm membranous; antennae 10-segmented to 11-segmented; legs much as in Icerya; beak short conical, one-segmented, with blunt-tipped, somewhat broadened, apical, sensory setae; thoracic spiracles large, with bar; with the three posterior pairs of abdominal spiracles, these simple, tubular; derm pores of the ordinary multilocular disk type only, no specially modified pores present; derm setae stiff, sparse, longer and more numerous along body margin; anal tube with a simple ring at inner end; with three oval ventral cicatrices placed close together.

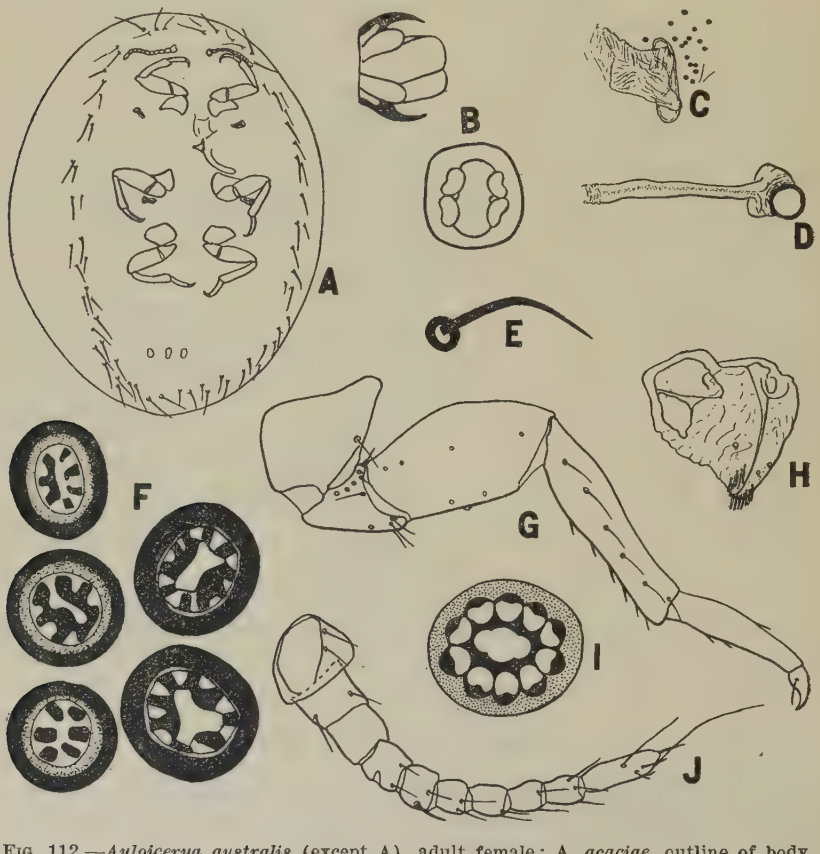

FIG. 112.—*Auloicerya australis* (except A), adult female: A, *acaciae*, outline of body, ventral, × 7.5; B, derm disk pore, surface and section, × 1,500; C, thoracic spiracle, × 230; D, abdominal spiracle, × 500; E, derm seta, × 500; F, various sorts of derm disk pores, × 1,500; G, leg, × 57.5; H, beak, × 230; I, ventral disk pores from area of vaginal opening, × 1,500; J, antenna, × 57.5

Larva.—Somewhat ovoid, broader anteriorly; antennae six-segmented, resembling those of Icerya; legs as in Icerya; beak one-segmented, short conical as in Icerya; thoracic spiracles with bar; abdominal spiracles minute, three pairs as in adult; derm pores of the ordinary multilocular disk type only; some derm setae quite small and inconspicuous, others very much enlarged and extremely prominent, the tips not acute, these including the two marginal and four to six dorsal rows; apical setae of normal form, elongate, slender, in three pairs, with the inner two setae more or less reduced, giving in one species an appearance of only two pairs present; anal tube with polygonal wax pores in and at inner end, and with ring of disk pores at mouth as in Icerya; apparently no ventral cicatrix in genotype, a single much reduced one in other species.

Adult male.—Very similar to this stage in Icerya as far as known. Some structural characteristics exhibited on the accompanying plate.

The two included species, which are described in some detail in the paper in which the genus was erected, offer some obvious con-

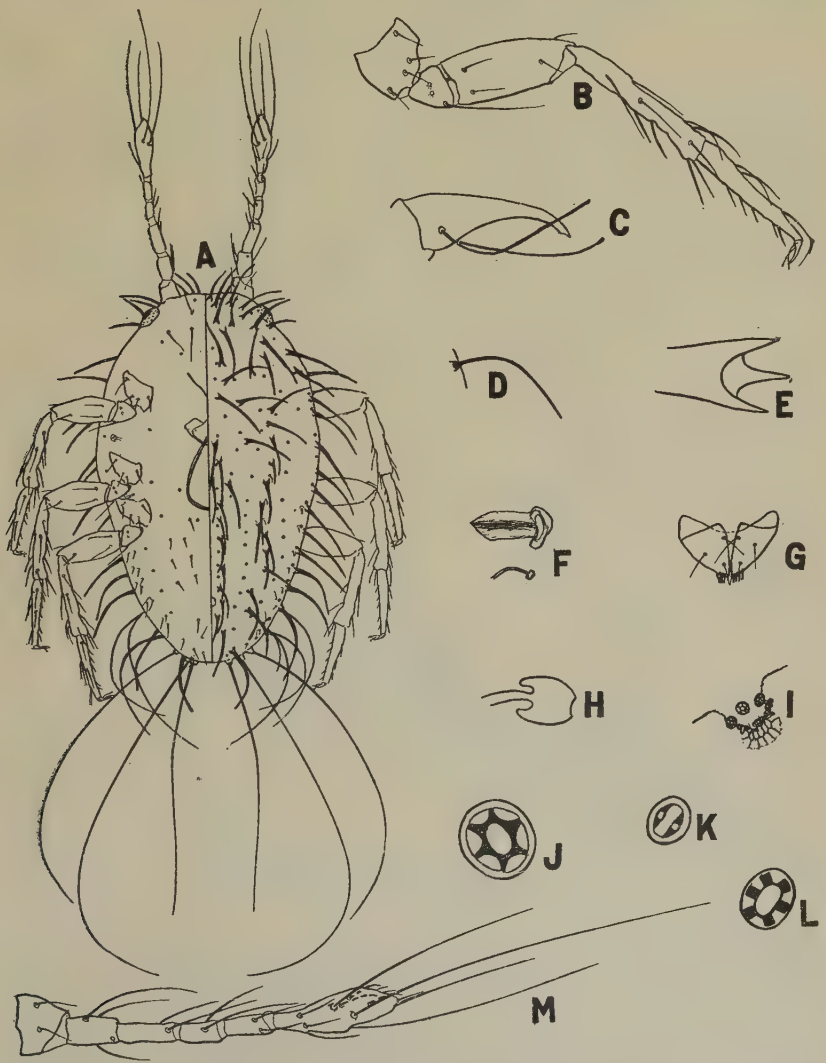

FIG. 113.—*Auloicerya australis*, larva: A, outline, dorsal and ventral, × 57.5; B, leg, × 115; C, claw, × 640; D, derm seta, × 115; E, tricuspidate apex of derm seta, × 1,500; F, thoracic and abdominal spiracles, × 230; G, beak, × 115; H, abdominal spiracle, × 1,500; I, anal tube, × 330; J, anal ring disk pore, × 1,500; K, ventral disk pore, × 1,500; L, dorsal disk pore, × 1,500; M, antenna, × 115

trasts, but appear to be close enough to permit their association in a single genus. They may be very readily separated in the first larval stage by the character of the apices of the enlarged setae, the tips of these in *australis* being tricuspid, while in *acaciae* they are bluntly rounded.

The known distribution of the genus includes the continent of Australia only.

No information is available regarding the life cycle or other biological characteristics of the included species. It seems probable that there is only a single generation annually.

Genus Steatococcus Ferris

(Pl. 7, F, and figs. 115 and 116)

This genus was established in 1921 by Ferris (*52, p. 69*), who definitely designated the species originally known as *Palaeococcus*

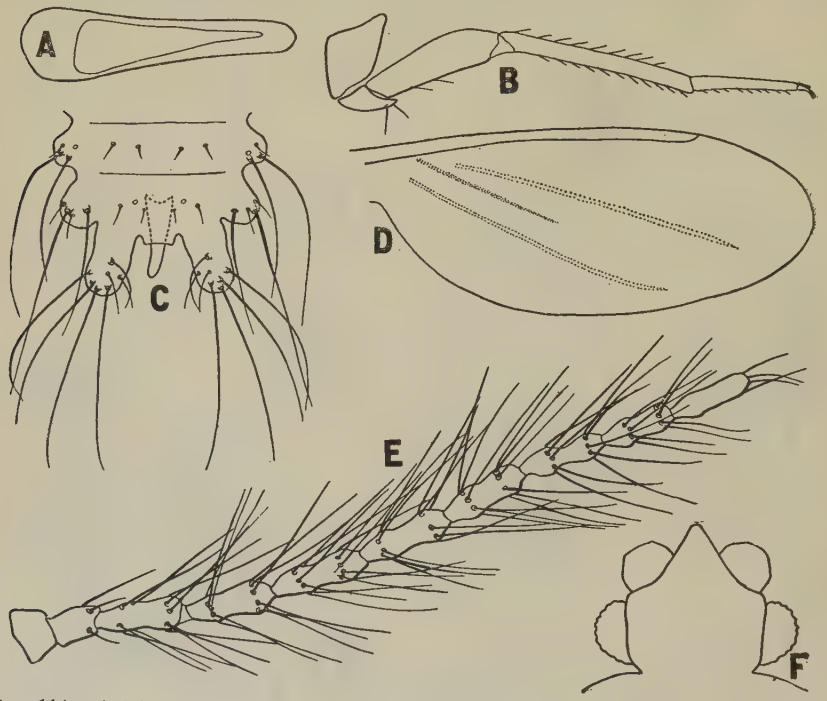

Fig. 114.—*Auloicerya australis*, adult male: A, penis sheath, × 115; B, leg, × 57.5; C, apex of abdomen, × 57.5; D, wing, × 30; E, antenna, × 57.5; F, head outline, × 57.5

morrilli Cockerell (*30*) as its type, and included with it the species previously known as *P. mexicanus* (Cockerell and Parrott) (*15, p. 4*), *P. plucheae* (Cockerell) (*10, p. 202*), *Steatococcus tabernicolus* Ferris (*52, p. 70*), and *P. townsendi* (Cockerell) (*10, p. 201*), all described from the Southwestern United States and northern Mexico. The present writer later assigned *P. nudatus* (Maskell) (*128, p. 405*) from Australia to the same genus, and a study of cotype and other specimens shows that *P. theobromae* Newstead (*147, p. 154*) and *Icerya euphorbiae* Brain (*3, p. 167*), African species, may also be included here, and *P. dymocki* Froggatt (*56, p. 36*), another Australian species, and finally a recently described species from New Guinea, *S. samaraius* Morrison (*136, p. 109*).[45]

[45] According to Vayssière (*170, p. 307*), who has examined specimens, *Palaeococcus caudatus* Newstead (*151, p. 6*) and *Aspidoproctus gowdeyi* Newstead (*152, p. 177*) belong in this genus.

GENERIC CHARACTERISTICS

Habit.—Living exposed on the branches of the host during the growing period; eggs deposited within a large internal marsupium having a median ventral opening.

FIG. 115.—*Steatococcus morrilli*, adult female: A, outline, optical section, × 7.5; B, base of largest type marginal seta, × 650; C, beak, × 60; D, leg, × 60; E, dorsal derm pore, × 650; F, anterior, and G, posterior, thoracic spiracles, × 60; H, abdominal spiracle, × 120; I, abdominal spiracle and adjacent derm pores, × 60; J, ventral cicatrices, × 30; K, antenna, × 60; L, disk pores from marsupial band, × 650; M, dorsal derm seta, × 650; N, body hair, × 650; O, body seta, × 650

Adult female.—Body externally with more or less secretion, this varying in quantity from small rounded tufts ranged in longitudinal rows to a fairly dense and uniform, more or less platelike coating completely concealing the derm; body ovoid in shape, distinctly broadened behind, with a marsupial

opening of varying shape ventrally immediately behind the posterior legs, this serving as a passage between a delicate internal marsupium, often filling the greater part of the body, and the exterior; derm mostly remaining membranous, in some species becoming more or less chitinized at maturity; antennae normally 9-segmented to 11-segmented, of the usual iceryine type; legs very similar to those of Icerya, the parts with relatively few setae, claw without

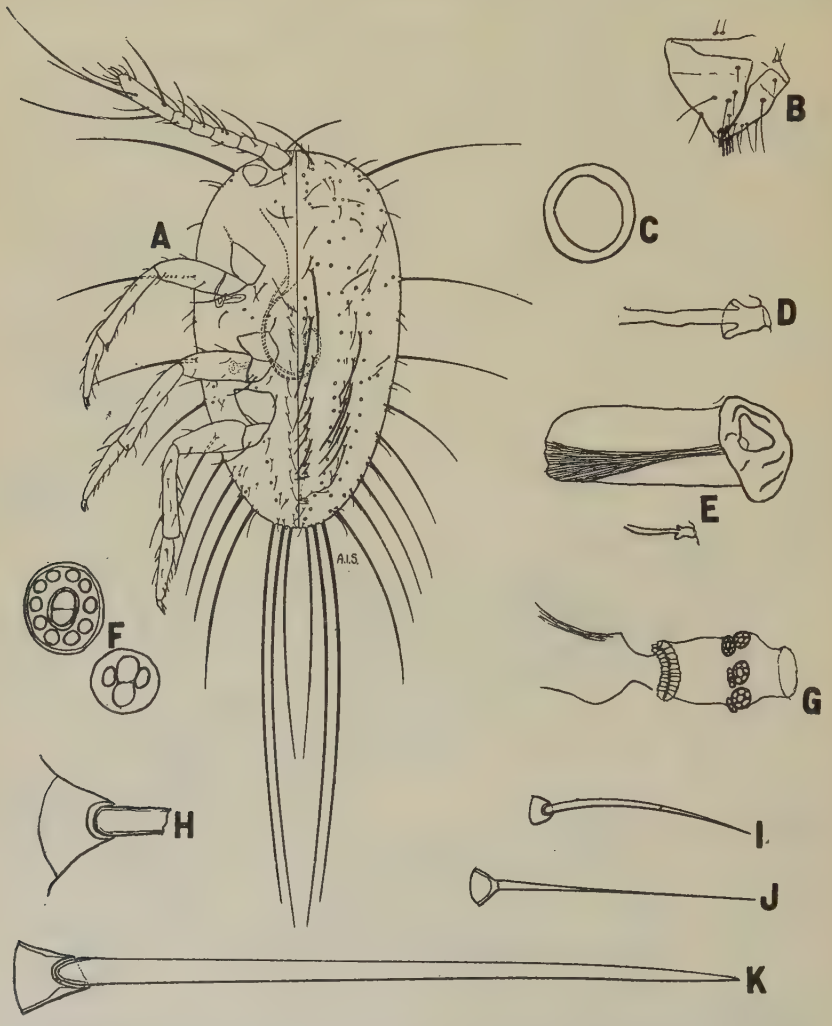

FIG. 116.—*Steatococcus morrilli*, larva: A, outline, dorsal and ventral, × 60; B, beak, × 115; C, ventral cicatrix, × 330; D, abdominal spiracle, × 1,280; E, thoracic and abdominal spiracles, × 460; F, dorsal and ventral derm disk pores, × 1,280; G, anal tube, × 330; H, base of marginal seta, × 650; I, ventral seta, × 650; J, dorsal hair, × 650; K, dorsal seta, × 650

denticle, claw digitules usually at least slightly exceeding the apex of the claw and faintly enlarged at tips; beak quite short conical, one-segmented, with a very faint suggestion of a joint close to base in some species; thoracic spiracles with bar but without pore cluster at opening; with three posterior pairs of simple tubular abdominal spiracles; derm with pores, the numbers showing much variation among the species, these pores varying somewhat in type, but in general resembling the sorts found in Icerya and including, in all the

species, rather small multilocular disk pores with oval, triangular, circular, or elongate centers and about nine loculi, and, in some species, a distinctly larger open-center type with six loculi, or a still larger type with triangular centers and six much smaller loculi arranged in pairs; derm setae with the usual basal collar as in Icerya, varying from slender, hairlike, to quite stout and spinelike, from pale in color to blackish, from relatively very sparse to relatively very abundant; hairs less numerous, slender, with hemispherical or conical bases; anal tube with a simple ring at inner end, the opening always surrounded by a more or less conspicuously developed cluster of setae and pores; ventral cicatrices varying in number from one to three, and in shape from circular to elliptical or somewhat kidneylike.

Preadult female.—Not available for any of the species.

Larva.—Elliptical in shape; antennae six-segmented, the apical much the longest, but only a little enlarged; legs rather slender, much as in Icerya; beak very stout conical, with blunt-tipped sensory setae; thoracic spiracular bar mostly slender; abdominal spiracles very small, simple as in Icerya; derm pores of the same general type as those described as characteristic for the adult stage, but smaller; derm setae varying from quite large and stout to quite small and slender, but the apical setae always in three definitely recognizable pairs, the middle one on each side always larger and longer, the other two varying from quite short and inconspicuous to nearly equal in length to the middle one, the lateral marginal varying considerably in conspicuousness; anal tube present, with a band of polygonal wax pores at inner end and a disjointed ring of disk pores at the opening; with a single, median, ventral cicatrix.

Adult male.—Unknown.

As already indicated in detail, the distribution of the species here included covers the Rocky Mountain subregion of the Nearctic region, the Austro-Malayan and Australian subregions of the Australasian region, and the West African and South African subregions of the Ethiopian region, a rather disjointed association, which suggests that a more complete segregation of the three elements included in the genus may be more nearly correct than the present arrangement.

There seems to be no precise information of any sort available regarding the life cycle of the members of this genus. Very probably one generation annually is produced.

The included species available for examination may be separated very readily on morphological characters into three definite groups, which are also separated by geographical segregation. The key which follows will serve both to separate and to characterize these three groups, which possibly are entitled to the status of subgenera.

Except for the species *mexicanus*, which is amply characterized by having an abundance of blackish dermal setae, the North American species are very difficult to segregate from one another, and no positive recognition characters have as yet been established, possibly because of the limited quantity of material thus far available for study purposes.

The following tentative key to the adult females of this genus is offered in the hope that it will be of some assistance in differentiating the species, although it will hardly be wholly satisfactory, since there are probably some still undescribed forms in the southwestern part of the United States.

KEY TO GROUPS AND SPECIES OF STEATOCOCCUS

Adult female

a. Marsupial opening with a complete circular to oval chitinized ring; derm pores of the one type only, small multilocular disk, with circular to elongate centers; (North American)----------(Group 1)

b. Body setae relatively very numerous, crowded, blackish in color. *mexicanus* (Cockerell and Parrott)

bb. Body setae relatively much less abundant, not blackish or crowded.

c. Body almost wholly destitute of setae, only a few along margin, around anal opening, etc., remaining----------*tabernicolus* Ferris

cc. Body setae more numerous and more widely distributed, but not conspicuous.

d. All body setae stout, many almost spinelike--*morrilli* (Cockerell)

dd. Body setae more slender, hairlike (*plucheae* Cockerell appears to be a synonym)----------*townsendi* (Cockerell)

aa. Marsupial opening ring incompletely chitinized anteriorly, its shape varying, but not completely circular or oval; derm with some pores of larger size and specialized type; (not American).

e. Derm with large and conspicuous "open-center" pores present along margins of body at least; (Australasian). (Group 2)

f. With a middorsal longitudinal cluster of large "open-center" disk pores; ring of marsupial opening wholly obliterated in front, the chitinized posterior section semicircular to somewhat elongate half-oval. *nudatus* (Maskell)

ff. Clusters of large "open-center" pores present along the body margin only; ring of marsupial opening large, elongate to half-oval, completed anteriorly not by a chitinized band but by a narrow band of disk pores. *samaraius* Morrison

ee. Derm without large and conspicuous "open-center" pores, only one type, circular with trilocular center and six or more loculi usually in pairs or groups, this type large or small; (African)----------(Group 3)

g. Marsupial opening transversely half-oval, incomplete anteriorly; disk pores small. *euphorbiae* (Brain)

gg. Marsupial opening triangular with closed apex posteriorly and lateral wings anteriorly; derm disk pores very large and conspicuous. *theobromae* (Newstead)

LIST OF GENERIC NAMES ASSIGNED TO THE FAMILY

A list of the generic names previously published in this family is given in Table 1, together with an indication of the present status of each, so far as this has been determined.

At least one stage of some species of every genus *not* marked with an asterick (*) has been examined; no examples of any stage have been available for the starred genera.

TABLE 1.—*List of generic names assigned to the family Margarodidae*

Name	Author	Distribution	Genotype	Current status	Assignment in this bulletin
Americoccus	MacGillivray	California	Matsucoccus fasciculensis Herbert	Americoccus	=Matsucoccus (Tribe Matsucoccini).
Aspidoproctus	Newstead	Africa	Walkeriana pertinax Newstead	Aspidoproctus	Aspidoproctus (Tribe Monophlebini).
Auloicerya	Morrison	Australia	Icerya rosae var. australis Maskell	Auloicerya	Auloicerya (Tribe Iceryini).
Callipappus	Guérin-Méneville	do	Callipappus westwoodi Guérin	Callipappus	Callipappus (Tribe Callipappini).
Clypeococcus	Newstead	Brazil	Icerya hempeli Cockerell	Clypeococcus	=Mimosicerya (Tribe Coelostomidiini).
Cockerelliella	MacGillivray	Philippine Islands	Monophlebulus townsendi Cockerell	Cockerellella	=Drosicha (Tribe Drosichini).
Coelostomidia	Cockerell	New Zealand	Coelostoma zealandicum Maskell	Coelostomidia	Coelostomidia (Tribe Coelostomidiini).
Coelostoma	Maskell	do	do	=Coelostomidia	=Coelostomidia (Tribe Coelostomidiini).
Crossotosoma	Douglas	Egypt	Crossotosoma aegyptiacum Douglas	=Icerya	=Icerya (Tribe Iceryini).
Crypticerya	Cockerell	Florida, Caribbean region	Icerya rosae Riley & Howard	=Palaeococcus	=Crypticerya (Tribe Iceryini).
Cryptokermes	Hempel	Brazil, Mexico	Cryptokermes brasiliensis Hempel	Cryptokermes	Cryptokermes (Tribe Coelostomidiini).
Drosicha	Walker	Eastern and southeastern Asia and adjacent islands.	Drosicha contrahens Walker	Drosicha	Drosicha (Tribe Drosichini).
Drosichiella	Morrison	Indian	Monophlebus tamarindus Green	Drosichiella	Drosichiella (Tribe Drosichini).
Drosichoides	do	Indo-Malayan	Llaveia haematoptera Cockerell	Drosichoides	Drosichoides (Tribe Drosichini).
Greenacoccus	MacGillivray	India	Monophlebus stebbingii Stebbing	Greenacoccus	=Drosicha (Tribe Drosichini).
Greeniella	do	do	do	do	Do.
Guerinia	Targioni-Tozzetti	Western Mediterranean region.	Coccus serratulae Fabricius	=Gueriniella	=Gueriniella (Tribe Iceryini).
Gueriniella	Fernald	do	do	Gueriniella	Gueriniella (Tribe Iceryini).
Hemaspidoproctus	Morrison	Indian	Aspidoproctus cinerea Green	Hemaspidoproctus	Hemaspidoproctus (Tribe Monophlebini).
Icerya	Signoret	World-wide	Dorthezia seychellarum Westwood	Icerya	Icerya (Tribe Iceryini).
Kuwania	Cockerell	Japan	Sasakia quercus Kuwana	Kuwania	Kuwania (Tribe Kuwaniini).
Labioproctus	Green	Ceylon	Walkeriana poleii Green	Labioproctus	Labioproctus (Tribe Monophlebini).
*Leachia	Signoret	Europe	Monophlebus fuscipennis Burmeister	=Palaeococcus	=Palaeococcus (Tribe Monophlebini).
Llaveia	do	Mexico, Central America	Coccus axin Llave	Llaveia	Llaveia (Tribe Llaveiini).
Llaveiella	Morrison	Mexico	Llaveia axin of Cockerell (not Llave)	Llaveiella	Llaveiella (Tribe Llaveiini).
Lophococcus	Cockerell	Africa	Lophococcus mirabilis Cockerell	=Aspidoproctus	=Aspidoproctus (Tribe Monophlebini)
Marchalina	Vayssière	Eastern Mediterranean region.	Monophlebus hellenicus Gennadius	Marchalina	Marchalina (Tribe Marchalinini).
Margarodes	Guilding	Lesser Antilles to world-wide.	Margarodes formicarum Guilding	Margarodes	Margarodes (Tribe Margarodini).
Matsucoccus	Cockerell	Japan, United States	Xylococcus matsumurae Kuwana	Matsucoccus	Matsucoccus (Tribe Matsucoccini).
Mimosicerya	do	Brazil	Icerya hempeli Cockerell	=Palaeococcus or Clypeococcus.	=Mimosicerya (Tribe Coelostomidiini).
Monophlebidus	Morrison	India	Monophlebidus indicus Morrison	Monophlebidus	Monophlebidus (Tribe Monophlebini).
Monophleboides	do	Africa	Monophlebus gymnocarpi Hall	Monophleboides	Monophleboides (Tribe Monophlebini).
Monophlebulus	Cockerell	Australia	Monophlebus fuscus Maskell	Monophlebulus	Monophlebulus (Tribe Monophlebulini).
*Monophlebus	Burmeister	Java	Monophlebus atripennis Burmeister	Monophlebus	Monophlebus (Tribe Monophlebini).
Neogreenia	MacGillivray	Ceylon	Monophlebus zeylanicus Green	Neogreenia	=Tribe Kuwaniini (generic status unsettled).
Neomargarodes	Green	Algeria	Neomargarodes erythrocephala Green	Neomargarodes	Neomargarodes (Tribe Margarodini).
Neosteingelia	Morrison	Nearctic, Alleghenian subregion.	Neosteingelia texana Morrison	Neosteingelia	Neosteingelia (Tribe Kuwaniini).
*Newsteadiella	MacGillivray	India	Icerya formicarum Newstead	Newsteadiella	Immature Icerya probably (Tribe Iceryini).
Nietnera	Green	Ceylon	Nietnera pundaluoya Green	Nietnera	Nietnera (Tribe Monophlebini).

TABLE 1.—*List of generic names assigned to the family Margarodidae*—Continued

Name	Author	Distribution	Genotype	Current status	Assignment in this bulletin
Nodulicoccus	Morrison	Australia	Monophlebus crawfordi var. levis Maskell.	Nodulicoccus	Nodulicoccus (Tribe Monophlebulini).
Ortonia	Signoret	Mexico, Central America	Ortonia bouvari Signoret	=Llaveia	=Llaveia (Tribe Llaveiini).
*Palaeococcus	Cockerell	Europe	Monophlebus fuscipennis Burmeister	Palaeococcus	Palaeococcus (Tribe Monophlebini).
Paracoelostoma	Morrison	Neotropical	Paracoelostoma peruviana Morrison	Paracoelostoma	Paracoelostoma (Tribe Coelostomidiini).
Paragreenia	MacGillivray	Ceylon	Monophlebus zeylanicus Green	=Neogreenia	=Tribe Kuwaniini (generic status unsettled).
Perissopneumon	Newstead	India and adjacent	Perissopneumon ferox Newstead	=Stigmacoccus	=Perissopneumon (Tribe Monophlebini).
Platycoelostoma	Morrison	New Zealand	Coelostoma compressa Maskell	Platycoelostoma	Platycoelostoma (Tribe Platycoelostomini).
Porphyrophora	Brandt	Europe	Not certain	=Margarodes	=Margarodes (Tribe Margarodini).
Proticerya	Cockerell	Southwestern part of United States and Mexico.	Icerya rileyi Cockerell	=Icerya	=Icerya (Tribe Iceryini).
Protortonia	Townsend	Mexico and Central America	Ortonia (Protortonia) primitiva Townsend.	=Llaveia	=Protortonia (Tribe Llaveiini).
Pseudaspidoproctus	Morrison	Africa	Aspidoproctus hyphaeniacus Hall	Pseudaspidoproctus.	Pseudaspidoproctus (Tribe Monophlebini).
Sasakia	Kuwana	Japan	Sasakia quercus Kuwana	=Kuwania	=Kuwania (Tribe Kuwaniini).
Sphaeraspis	Giard	South Africa	Sphaeraspis capensis Giard	=Margarodes	=Margarodes (Tribe Margarodini).
Steatococcus	Ferris	Southwestern part of United States and Mexico, Australia, Africa.	Palaeococcus morrilli Cockerell	Steatococcus	Steatococcus (Tribe Iceryini).
Steingelia	Nassanow	Europe	Steingelia gorodetskia Nassanow	Steingelia	Steingelia (Tribe Steingeliini).
Stigmacoccus	Hempel	Brazil	Stigmacoccus asper Hempel	Stigmacoccus	Stigmacoccus (Tribe Stigmacoccini).
Stomacoccus	Ferris	California	Stomacoccus platani Ferris	Stomacoccus	Stomacoccus (Tribe Steingeliini).
*Tessarobelus	Montrouzier	New Caledonia	Tessarobelus guerinii Montrouzier	Tessarobelus	Tessarobelus (Tribe ? Monophlebulini, status uncertain).
Ultracoelostoma	Cockerell	New Zealand	Coelostoma assimile Maskell	Ultracoelostoma	Ultracoelostoma (Tribe Coelostomidiini).
Walkeriana	Signoret	Ceylon	Coccus floriger Walker	Walkeriana	Walkeriana (Tribe Monophlebini).
Warajicoccus	Kuwana	Japan	Monophlebus corpulentus Kuwana	Warajicoccus	=Drosicha (Tribe Drosichini).
Xylococculus	Morrison	Nearctic	Xylococcus betulae Pergande	Xylococculus	Xylococculus (Tribe Xylococcini).
Xylococcus	Löw	Palaearctic	Xylococcus filiferus Löw	Xylococcus	Xylococcus (Tribe Xylococcini).

LIST OF SPECIFIC NAMES ASSIGNED TO THE FAMILY

Table 2 gives a list of the species names previously published in this family, together with an indication of the present status of each, so far as this has been determined.

Some stage of each species marked with an asterisk (*) has been examined during the course of this work.

TABLE 2.—*List of specific names assigned to the family Margarodidae*

Original species name	Author	Distribution	Original generic assignment	Current generic and specific assignment	Generic and specific assignment according to this bulletin
*abrahami	Newstead	British Guiana	Llaveia	Llaveia	Crypticerya.
*acaciae	Morrison and Morrison	Australia	Auloicerya	Auloicerya	Auloicerya.
acaciae	Joubert	South Africa	Monophlebus	Monophlebus	? Pseudaspidoproctus.
*acalyptus	Herbert	Idaho	Matsucoccus	Matsucoccus	Matsucoccus.
adipofera	Dondé Ruiz	Mexico	Coccus	Llaveia axin	Llaveia axin.
*aegyptiaca	Douglas	Egypt, India	Crossotosoma	Icerya	Icerya.
*africana	Newstead	Kilimandjaro	Walkeriana	Walkeriana	Pseudaspidoproctus.
africanus	do	German Southwest Africa	Monophlebus	Monophlebus	?: possibly Monophleboides.
*albolutea, seychellarum	Cockerell	West Africa	Icerya	Icerya	Icerya albolutea.
*alni	Oguma	Japan	Xylococcus	Xylococcus	Xylococcus japonicus.
Do	Florence	California	do	do	Xylococculus.
*andreae	Green	Congo Region	Walkeriana	Walkeriana	preadult Aspidoproctus.
anonae	Newstead		Steatococcus	Can find no data on this insect. (See Vayssière, *170*.)	
armatus	do	German East Africa	Aspidoproctus	Aspidoproctus	Aspidoproctus.
armeniaca	Burmeister	Armenia	Porphyrophora	Margarodes hamelii	Margarodes hamelii.
*asper	Hempel	Brazil, Guiana	Stigmacoccus	Stigmacoccus	Stigmacoccus.
*assimile	Maskell	New Zealand	Ultracoelostoma	Ultracoelostoma	Ultracoelostoma.
atripennis	Burmeister	Java	Monophlebus	Monophlebus	Monophlebus.
*australe	Maskell	Australia	Coelostoma	Callipappus	Callipappus.
*australis, rosae	do	do	Icerya	Palaeococcus	Auloicerya.
axin	Llave	Mexico	Coccus	Llaveia	Llaveia.
axin dorsalis	Dugès	do	Monophlebus	do	Llaveia ? axin.
axinus	Sallé	do	Coccus	Llaveia axin	Llaveia axin.
azteca	Ferris	do	Marchalina	Marchalina	?.
*benguetensis	Cockerell	Philippine Islands	Llaveia	Llaveia	Drosicha.
*betulae	Pergande	Eastern part of United States	Xylococcus	Xylococcus	Xylococculus.
bicolor	Newstead	Gold Coast	Palaeococcus	Palaeococcus	Crypticerya (Vayssière, *170*).
bouvari	Signoret	Guatemala	Ortonia	Llaveia	Llaveia.
bouvieri	Vayssière	French Equatorial Africa	Aspidoproctus	Aspidoproctus	Aspidoproctus.
*brasiliensis	Hempel	Brazil	Cryptokermes	Cryptokermes	Cryptokermes.
Do	do	do	Icerya	Icerya	Icerya.
brasiliensis	Wille	do	Margarodes	Margarodes	Margarodes.
brasiliensis	Walker	do	Monophlebus	Palaeococcus	?.
*britannica	Green	England	Kuwania	Steingelia gorodetskia	Steingelia gorodetskia.
bufo	Fuller	Australia	Callipappus	Callipappus	Callipappus.
burmeisteri	Westwood	?	Monophlebus	Drosicha	Drosicha.
buxtoni	Newstead	Algeria	Margarodes	Margarodes	Margarodes
*cacti	Linnaeus	St. Eustatius, Lesser Antilles.	Coccus	Llaveia	Protortonia.
cajani	Newstead	Nigeria	Palaeococcus	Palaeococcus	Crypticerya (Vayssière, *170*).
*callitri	Froggatt	Australia	Llaveia	Llaveia	Icerya.
*candida	Cockerell	Philippine Islands	Icerya	Icerya	Icerya seychellarum.
*capensis	Giard	South Africa	Margarodes (Sphaeraspis)	Margarodes	Margarodes.
carinatus	Lindinger	German East Africa	Lophococcus	Lophococcus	Aspidoproctus.
cassiae	Laing, nomen nudum		Aspidoproctus		(?: See Vayssière, *170*),

caudatus	Newstead	Uganda	Palaeococcus	Palaeococcus	Steatococcus (Vayssière, *170*).
championi	Cockerell	Panama	Monophlebus	Tessarobelus	Llaveiini, genus uncertain.
chilensis	Hempel	Chile	Icerya	Icerya	Icerya.
*cinerea	Green	India	Walkeriana	Aspidoproctus	Hemaspidoproctus.
citriperda, purchasi	Hempel	Brazil	Icerya	Icerya	Icerya.
*colimensis	Cockerell	Mexico	do	do	Do.
*compacta	Green	Ceylon	Walkeriana	Walkeriana	Walkeriana.
*comperei	Morrison & Morrison	Australia	Monophlebulus	Monophlebulus	Monophlebulus.
*compressum	Maskell	New Zealand	Coelostoma	Coelostomidia	Platycoelostoma.
congolensis	Vayssière	Belgian Congo	Aspidoproctus	Aspidoproctus	Aspidoproctus.
*contrahens	Walker	North China	Drosicha	Drosicha	Drosicha.
*convexus	Morrison	Philippine Islands	Lophococcus	Lophococcus	Perissopneumon.
*corpulentus	Kuwana	Japan	Monophlebus	Warajicoccus	Drosicha.
corticalis	Vayssière	Belgian Congo	Icerya	Icerya	Icerya.
*crawfordi	Maskell	Australia	Monophlebus	Drosicha	Monophlebulus.
*crawfordi levis	do	do	do	do	Nodulicoccus levis.
*crawfordi pilosior	do	do	do	do	Monophlebulus pilosior.
*crawii, purchasi	Cockerell	California	Icerya	Icerya	Icerya.
cristata, seychellarum	Newstead	Madagascar	do	do	Do.
*crocea	Green	Ceylon	do	Icerya seychellarum	Icerya seychellarum.
*dalbergiae	Stebbing	India	Monophlebus	Monophlebus	Drosicha.
digitifrons	Newstead	Uganda	Walkeriana	Walkeriana	?
dorsalis, axin	Dugès	Mexico	Monophlebus	Llaveia	Llaveia ?axin.
dubius	Fabricius	Sumatra	Chironomus	Monophlebus	?
dugesi	Vayssière	Mexico	Monophlebus	do	Llaveia axin (Vayssière, *170*).
*dymocki	Froggatt	Australia	Palaeococcus	Palaeococcus	Steatococcus.
ellenbergeri	Vayssière	Upper Zambesi	Aspidoproctus	Aspidoproctus	Aspidoproctus.
erythrocephala	Green	Algeria	Neomargarodes	Neomargarodes	Neomargarodes.
*euphorbiae	Brain	South Africa	Icerya	Icerya	Steatococcus.
Do	Green	Ceylon	Walkeriana	Aspidoproctus	Hemaspidoproctus.
ewarti	Newstead	West Africa	Icerya	Palaeococcus	Crypticerya.
fabricii	Westwood	Sumatra	Monophlebus	Monophlebus dubius Fab.	Monophlebus dubius Fab.
farinosus	Fuller	Australia	Callipappus	Callipappus	Callipappus.
*fasciculensis	Herbert	California	Matsucoccus	Matsucoccus	Matsucoccus.
ferox	Newstead	India	Perissopneumon	Stigmacoccus	Perissopneumon.
festiva	Kieffer	do	Leachia	Icerya minor Green	?Icerya minor Green.
ficus	Laing, nom. nud		Monophlebus		(See Vayssière, *170*).
*filiferus	Löw	Austria	Xylococcus	Xylococcus	Xylococcus.
flava	Hempel	Brazil	Icerya	Icerya	Icerya.
*floriger	Walker	Ceylon	Coccus	Walkeriana	Walkeriana.
*formicarum	Guilding	Lesser Antilles	Margarodes	Margarodes	Margarodes.
formicarum	Newstead	India	Icerya	Newsteadiella	?Icerya.
fortis	Cockerell	Natal	Monophlebus	?Monophlebus	?Pseudaspidoproctus.
frischii	Brandt	Europe	Porphyrophora	Margarodes polonicus	=Margarodes polonicus.
*fulleri	Cockerell	Natal	Monophlebus	?Monophlebus	Pseudaspidoproctus.
*furcatus	Green	Ceylon	do	Monophlebus	?:perhaps Walkeriana.
fuscipennis	Burmeister	Europe	do	Palaeococcus	Palaeococcus.
*fuscus	Maskell	Australia	do	Monophlebulus	Monophlebulus.
gallicus	Signoret	France	Porphyrophora	Margarodes	Margarodes polonicus (Lindinger, *113*).
genistae	Hempel	Brazil	Icerya	Icerya	Icerya.
ghesquierei	Vayssière	Belgian Congo	Aspidoproctus	Aspidoproctus	Aspidoproctus.

TABLE 2.—*List of specific names assigned to the family Margarodidae*—Continued

Original species name	Author	Distribution	Original generic assignment	Current generic and specific assignment	Generic and specific assignment according to this bulletin
giganteus	Newstead	Nigeria	Aspidoproctus	Aspidoproctus	Aspidoproctus.
glaber	Lindinger	German East Africa	Lophococcus	Lophococcus	Do.
*gorodetskia	Nassanow	Europe	Steingelia	Steingelia	Steingelia.
gowdeyi	Newstead	Uganda	Aspidoproctus	Aspidoproctus	Steatococcus. (Vayssière, *170*).
greeni	Brain	South Africa	Margarodes	Margarodes	Margarodes.
guerinii	Montrouzier	New Caledonia	Tessarobelus	Tessarobelus	? Monophlebulini, status uncertain.
gymnocarpi	Hall	Egypt	Monophlebus	Monophlebus	Monophleboides.
*haematoptera	Cockerell	Borneo	Llaveia	Llaveia	Drosichoides.
hamelii	Brandt	Armenia	Coccus	Margarodes	Margarodes.
*hellenicus	Gennadius	Greece	Monophlebus	Palaeococcus	Marchalina.
*hempeli	Cockerell	Brazil	Icerya	do	Mimosicerya.
*hiemalis	do	New Mexico	Margarodes	Margarodes	Margarodes.
hirculus	Green, nom. nud	Ceylon (actually Australian)	Monophlebus	Monophlebus	Auloicerya acaciae (in Vayssière, *170*).
*hirsutissimus	Hall	Egypt	Margarodes	Margarodes	Margarodes.
hirticornis	Fonscolombe	Europe	Coccus	?Palaeococcus	?
hirtus	Brain	Cape Province	Monophlebus	Monophlebus	?:perhaps Monophleboides.
*howardi	Kuwana	Japan	Warajicoccus	Warajicoccus	Drosicha.
hyperici	Froggatt	New South Wales	Icerya	Icerya	?
*hyphaeniacus	Hall	Egypt	Aspidoproctus	Labioproctus	Pseudaspidoproctus.
illigeri	Westwood	Tasmania	Monophlebus	?Monophlebus	? Monophlebulini, genus uncertain.
*immane	Maskell	Australia	Coelostoma	Callipappus	Callipappus.
*indicus	Green	India	Margarodes	Margarodes	Margarodes.
Do	Morrison	do	Monophlebidus	Monophlebidus	Monophlebidus.
insulans	Hempel	Brazil	Icerya	Icerya	?
*jacobsoni	Green	Java	do	do	Crypticerya.
japonicus	Oguma	Japan	Xylococcus	Xylococcus	Xylococcus.
*koebelei	Maskell	Australia	Icerya	Icerya	Icerya.
*larreae, rileyi	Cockerell	Mexico	do	do	Do.
leachii	Westwood	India	Monophlebus	Drosicha	Drosicha.
*levis, crawfordi	Maskell	Australia	do	do	Nodulicoccus levis.
*lichenoides	Cockerell	Philippine Islands	Drosicha	do	Drosicha townsendi.
*littoralis	do	Mexico	Icerya	Icerya	Icerya.
*littoralis mimosae	do	do	do	do	Do.
*littoralis tonilensis	do	do	do	do	Do.
*longisetosa	Newstead	German East Africa	do	do	Do.
luederwaldti	Hempel	Brazil	do	do	Do.
*luzonica	Cockerell	Philippine Islands	Llaveia	Llaveia	Drosicha townsendi.
*macrocarpae	Coleman	California	Xylococcus	Xylococcus	Xylococculus.
*mangiferae, stebbingii	Green	India	Monophlebus	Monophlebus	Drosicha mangiferae.

*margarodes	Burmeister	Lesser Antilles	Porphyrophora		Margarodes formicarum.
*maskelli	Cockerell	China	Monophlebus	Drosicha	Drosicha.
*maskelli, purchasi	do	California	Icerya	Icerya	Icerya.
*matsumurae	Kuwana	Japan	Xylococcus	Matsucoccus	Matsucoccus.
*maxima	Newstead	Gold Coast	Icerya	Icerya	Icerya.
*maximus	Lounsbury	Rhodesia, German East Africa.	Aspidoproctus	Aspidoproctus	Aspidoproctus.
maynei	Vayssière	Belgian Congo	Icerya	Icerya	Icerya.
*mediterraneus	Silvestri	Italy	Margarodes	Margarodes	Margarodes.
*meridionalis	Morrison	Southeastern United States	do	do	Do.
*mexicanorum	Cockerell	Mexico	Ortonia	Llaveia	Llaveia.
*mexicanus	Morrison	do	Cryptokermes	Cryptokermes	Cryptokermes.
*mexicanus, rosae	Cockerell	do	Crypticerya	Palaeococcus	Steatococcus.
mimeuri	Vayssière	French West Africa	Aspidoproctus	Aspidoproctus	Aspidoproctus.
*mimosae, littoralis	Cockerell	Mexico	Icerya	Icerya	Icerya.
*minima	Morrison	Argentina	do	do	Do.
*minor	Green	India	do	do	Do.
*mirabilis	Cockerell	Natal	Lophococcus	Lophococcus	Aspidoproctus.
*mirabilis tricornis	Newstead	German Southwest Africa	do	Aspidoproctus	Do.
*montserratensis	Riley and Howard	West Indies	Icerya	Icerya	Icerya.
*morrilli	Cockerell	Arizona	Palaeococcus	Steatococcus	Steatococcus.
napiformis	Kuwana	Japan	Xylococcus	Xylococcus	?Xylococcus.
*nardi, seychellarum	Green	Ceylon	Icerya	Icerya	Icerya nardi.
*natalensis	Douglas	Natal	Ortonia	do	Crypticerya.
neavei	Newstead	Nyassaland	Aspidoproctus	Aspidoproctus	Aspidoproctus.
newsteadi	Brain	South Africa	Margarodes	Margarodes	Margarodes.
*niger	Green	India	do	do	Neomargarodes.
nigroareolata	Newstead	Uganda	Icerya	Icerya	Icerya.
niveus	Hempel	Brazil	Monophlebus	Monophlebus	?
*nudatus	Maskell	Australia	Icerya	Palaeococcus	Steatococcus.
*oaxacoensis	Morrison	Mexico	Llaveia	Llaveia	Llaveia.
*octocaudata, stebbingi	Green	India	Monophlebus	Monophlebus	Drosicha mangiferae.
*okadae	Kuwana	do	Icerya	Icerya seychellarum	Icerya seychellarum.
*ovilla	Green	Ceylon	Walkeriana	Walkeriana	Walkeriana.
*palavanica	Cockerell	Philippine Islands	Drosicha	Drosicha	Drosicha.
pallidus	Newstead	Kilimandjaro	Monophlebus	Monophlebus	?: perhaps Aspidoproctus.
*palmeri	Riley and Howard	Mexico	Icerya	Icerya	Icerya.
*papillosus	Green	India	Margarodes	Margarodes	Margarodes.
parieli	Vayssière	Morocco	do	do	Do.
parvus	Lindinger	German East Africa	Lophococcus	Lophococcus	Aspidoproctus.
pattersoni, sulfurea	Newstead	Gold Coast	Icerya	Icerya	Icerya.
paulista	Hempel	Brazil	do	do	?
peringueyi	Brain	South Africa	Margarodes	Margarodes	Margarodes.
perrisii	Signoret	France	Porphyrophora	do	Margarodes polonicus (Lindinger, *113*).
*pertinax	Newstead	Central Africa	Walkeriana	Aspidoproctus	Aspidoproctus.
*peruviana	Morrison	Peru	Paracoelostoma	Paracoelostoma	Paracoelostoma.
*philippinensis	Green	Philippine Islands	Monophlebus	Monophlebus	Drosicha townsendi.
*phyllanthi	do	Ceylon, India	do	do	Drosichiella.
*pilosa	do	Ceylon	Icerya	Icerya	Icerya.
Do	Maskell	New Zealand	Coelostoma	Coelostomidia	Coelostomidia.
*pilosior, crawfordi	do	Australia	Monophlebus	Drosicha	Monophlebulus pilosior.

TABLE 2.—*List of specific names assigned to the family Margarodidae*—Continued

Original species name	Author	Distribution	Original generic assignment	Current generic and specific assignment	Generic and specific assignment according to this bulletin
pimentae, primitiva	Newstead	Jamaica	Llaveia	Llaveia	Crypticerya pimentae.
*pini	Green	England	Kuwania	Kuwania	Matsucoccus matsumurae.
*pinicola	Kuwana	Japan	Warajicoccus	Warajicoccus	Drosicha.
*platani	Ferris	California	Stomacoccus	Stomacoccus	Stomacoccus.
*plucheae, townsendi	Cockerell	New Mexico	Icerya	Steatococcus	Steatococcus plucheae.
*polii	Green	Ceylon	Walkeriana	Labioproctus	Labioproctus.
polonicus	Linnaeus	Europe	Coccus	Margarodes	Margarodes.
*primitiva	Townsend	Mexico	Ortonia	Llaveia	Protortonia.
primitiva pimentae	Newstead	Jamaica	Llaveia	do	Crypticerya pimentae.
*pulcher	Leonardi	Java	Palaeococcus	Palaeococcus	Icerya.
*pundaluoya	Green	Ceylon	Nietnera	Nietnera	Nietnera.
*purchasi	Maskell	Australia, world wide	Icerya	Icerya	Icerya.
purchasi citriperda	Hempel	Brazil	do	do	Do.
*purchasi crawii	Cockerell	California	do	do	Do.
*purchasi maskelli	do	do	do	do	Do.
*quadricaudatus	Green	Ceylon	Monophlebus	Monophlebus	Drosicha.
*quercus	Ehrhorn	California	Xylococcus	Xylococcus	Xylococculus.
Do	Kuwana	Japan	Sasakia	Kuwania	Kuwania.
raddoni	Westwood	West Africa, Gold Coast	Monophlebus	?Monophlebus	?
*rileyi	Cockerell	New Mexico, Mexico	Icerya	Icerya	Icerya.
Do	Giard	Florida	Margarodes	Margarodes	Margarodes.
*rileyi larreae	Cockerell	Mexico	Icerya	Icerya	Icerya.
*rosae	Riley and Howard	Florida, West Indies	do	Palaeococcus	Crypticerya.
*rosae australis	Maskell	Australia	do	do	Auloicerya australis.
*rosae mexicanus	Cockerell	Mexico	Crypticerya	do	Steatococcus mexicanus.
ruber	Brain	South Africa	Margarodes	Margarodes	Margarodes.
*rubiginosus	Maskell	Australia	Coelostoma	Callipappus	Callipappus.
*sacchari	Guérin	Orient	Coccus	Icerya seychellarum	Icerya seychellarum.
*samaraius	Morrison	New Guinea	Steatococcus	Steatococcus	Steatococcus.
*sanguinea	Cockerell	Philippine Islands	Llaveia	Llaveia	Drosichoides.
saundersii	Westwood	"Oriental" India	Monophlebus	do	Drosicha.
schoutedeni	Vayssière	Belgian Congo	Icerya	Icerya	Icerya.
*schrottkyi	Hempel	Brazil	do	do	Do.
senex	Green	Ceylon	Walkeriana	Walkeriana	? : perhaps Hemaspidoproctus.
*serratulae	Fabricius	Europe, Algeria	Coccus	Gueriniella	Gueriniella.
serrei	Vayssière	Java	Aspidoproctus	Aspidoproctus	? : perhaps Perissopneumon.
*seychellarum	Westwood	Orient	Dorthezia	Icerya	Icerya.
*seychellarum albolutea	Cockerell	West Africa	Icerya	do	Icerya albolutea.
seychellarum cristata	Newstead	Madagascar	do	do	Icerya.
*seychellarum nardi	Green	Ceylon	do	do	Icerya nardi.
*similis	Morrison	Panama, Trinidad, Tobago	do	do	Icerya.
Do	do	Galapagos	Margarodes	Margarodes	Margarodes.

sjostedti	Newstead	Kilimandjaro	Monophlebus	Monophlebus	? : perhaps Monophleboides.
splendida	Lindinger	German East Africa	Icerya	Icerya	Icerya.
*stebbingii	Stebbing	India	Monophlebus	?Monophlebus	Drosicha.
*stebbingii mangiferae	Green	do	do	Monophlebus	Drosicha mangiferae.
*stebbingii octocaudata	do	do	do	do	Do.
suaedae	Vayssière	Tunis	do	do	? : perhaps Monophleboides.
*subandina	Leonardi	Argentina	Icerya	Icerya	Icerya.
*subterraneus	Morrison and Morrison	Australia	Monophlebulus	Monophlebulus	Monophlebulus.
*sulfurea	Lindinger	German East Africa	Icerya	Icerya	Icerya.
sulfurea pattersoni	Newstead	Gold Coast	do	do	Do.
tabayae	Lindinger	Canaries	Palaeococcus	Palaeococcus	?
*tabernicolus	Ferris	Lower California	Steatococcus	Steatococcus	Steatococcus.
*taenechina	Morrison	Mexico	Llaveiella	Llaveiella	Llaveiella.
*tamarindus	Green	India	Monophlebus	Monophlebus	Drosichiella.
tangalla	do	Ceylon	Icerya	Icerya aegyptiaca	Icerya aegyptiaca.
taunayi	Hempel	Brazil	Icerya	Icerya	?
*tectonae	Morrison	India	Drosichiella	Drosichiella	Drosichella.
*tectonae	Stebbing, nomen nudum	do	Monophlebus	Monophlebus	Drosichiella tectonae.
*texana	Morrison	Eastern United States	Neosteingelia	Neosteingelia	Neosteingelia.
*theobromae	Newstead	West Africa	Palaeococcus	Palaeococcus	Steatococcus.
*tonilensis, littoralis	Cockerell	Mexico	Icerya	Icerya	Icerya.
*townsendi	do	New Mexico	do	Steatococcus	Steatococcus.
Do	do	Philippine Islands	Monophlebulus	Monophlebulus	Drosicha.
*townsendi plucheae	do	New Mexico	Icerya	Steatococcus plucheae	Steatococcus plucheae.
*trabuti	Marchal	Algeria	Neomargarodes	Neomargarodes	Neomargarodes.
tremae	Vayssière	Belgian Congo	Icerya	Icerya	Icerya.
*tricornis, mirabilis	Newstead	German Southwest Africa	Lophococcus	Aspidoproctus	Aspidoproctus tricornis.
trilobitum	Reed	Chile	Margarodes	Margarodes vitium	Margarodes vitium.
*trimeni	Giard	South Africa	do	Margarodes	Margarodes.
*uhleri	Signoret	Ecuador	Ortonia	Llaveia	Probably represents a new genus; left under Llaveia for the present.
*variegatus	Green	Ceylon	Monophlebus	Monophlebus	Drosicha.
verrucosus	Newstead	Uganda	Aspidoproctus	Aspidoproctus	Aspidoproctus.
vitis	F. Phillipi	Chile	Heterodera	Margarodes vitium	Margarodes vitium.
*vitium	Giard	Chile, Argentina	Margarodes	Margarodes	Margarodes.
*vuilleti	Vayssière	West Africa	Lophococcus	Lophococcus	Aspidoproctus.
*wairoensis	Maskell	New Zealand	Coelostoma	Coelostomidia	Coelostomidia.
*westwoodi	Guérin	Australia	Callipappus	Callipappus	Callipappus.
xyliae	Green, nomen nudum	India	Callipappus	Walkeriana	Perissopneumon.
*zealandica	Maskell	New Zealand	Walkeriana	Coelostomidia	Coelostomidia.
*zeteki	Cockerell	Canal Zone	Coelostoma	Icerya	Icerya.
*zeylanicus	Green	Ceylon	Icerya	Kuwania	?
zimmermanni	Newstead	German East Africa	Monophlebus	Stigmacoccus	?
			Perissopneumon		

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INDEX

[Figures in bold-faced type indicate pages on which species, genera, and higher groups are defined]

abietis, 8.
abrahami, 203, 222.
acaciae, Auloicerya, 211, 212, 213, 222.
acaciae, Monophlebus, 140, 222.
acalyptus, 52, 53, 222.
adipofera, 222.
aegyptiaca, 203, 207, 208, **210,** 222.
africana, Pseudaspidoproctus, 140, 222.
africanus, Monophlebus, 127, 222.
albolutea, seychellarum, 207, 210, **211,** 222, 226.
alni (Florence), 45, 222.
alni (Oguma), 44, 222.
Americoccus, 48, 219.
andreae, 222.
anonae, 222.
armatus, 158, 222.
armeniaca, 222.
asper, 37, 38, 39, 222.
Aspidoproctus, 11, 14, 18, 19, 20, 21, 22, 26, 122, 123, 124, 132, 138, 140, 148, **151,** 214, 219.
assimile, 108, 109, 110, 111, 222.
atripennis, 129, 144, 222.
Auloicerya, 196, 197, **211,** 219.
australe, 222.
australis, Callipappus, 83, 84, 85, **86.**
australis, rosae, Auloicerya, 211, 212, 213, 214, 222, 226.
axin, Coccus, 183.
axin, Llaveia, 182, 183, 188, **189,** 192, 222.
axinus, 222.
azteca, 222.
benguetensis, 169, **170,** 188, 222.
betulae, 45, 46, 47, 222.
bicolor, 203, 222.
bouvari, 183, 188, **189,** 222.
bouvieri, 158, 222.
brasiliensis, Cryptokermes, 100, 101, 102, 103, **104,** 222.
brasiliensis, Icerya, 207, **211,** 222.
brasiliensis, Margarodes, 77, 222.
brasiliensis, Monophlebus, 129, 144, 222.
britannica, 55, 222.
bufo, 86, 222.
burmeisteri, 169, 222.
buxtoni, 77, **78,** 222.
cacti, 5, 189, 191, 192, 222.
cajani, 203, 222.
Callipappinae, 82.
Callipappini, 62, 63, **82.**
Callipappus, 11, 14, 18, 62, **82,** 219.
callitri, 189, **209,** 222.
candida, 208, 222.
capensis, 77, **78,** 222.
carinatus, 158, 222.
cassiae, 158, 222.
caudatus, 203, 214, 223.
championi, 223.
chilensis, 207, 223.
Chironomus, 145.
cinerea, 151, 223.
cinereus, 149, 150.
citriperda, purchasi, 208, 223, 226.
Clypeococcus, 105, 219.
Cockerellella, 163, 219.
Coccus, 5, 141, 183, 191, 197, 203.
Coelostoma, 35, 84, 86, 89, 108, 112, 219.
Coelostomidia, 35, 38, 96, 97, 111, **112,** 219.
Coelostomidiinae, 27, 28, 29, 33, 34, **86.**
Coelostomidiini, 12, 19, 21, 24, 88, **94,** 96.
colimensis, 208, **209,** 223.
compacta, 144, 223.
comperei, 176, 178, 179, 223.
compressa, 89, 90, 91.
compressum, 223.
congolensis, 158, 223.
contrahens, 163, 164, 165, 167, 168, **169,** 223.
convexa, 136, 137.
convexus, 138, 223.
corpulenta, 164, 165, 166, 167, 168, **169.**
corpulentus, 163, 223.
corticalis, 208, 223.
crawfordi, 173, 175, 176, 177, 178, 179, 223.
crawii, purchasi, 208, **209,** 223, 226.
cristata, seychellarum, 208, 223, 226.
crocea, 208, 223.
Crossotosoma, 203, 219.
Crypticerya, 10, 196, 197, **200,** 201, 208, 219.
Cryptokermes, 15, 16, 21, 96, 97, **100,** 106, 107, 108, 219.
Dactylopiinae, 37, 100.
dalbergiae, 169, **170,** 223.
digitifrons, 223.
dorsalis, axin, 188, 222, 223.
Dorthezia, 203.
Drosicha, 7, 10, 18, 19, 21, 24, 26, 122, 124, 145, 155, 158, 160, 161, 162, **163,** 169, 171, 172, 189, 203, 219.
Drosichiella, **160,** 219.
Drosichini, 120, 122, **158,** 160, 189.
Drosichoides, 160, **171,** 219.
dubius, 145, 223.
dugesi, 189, 223.
dymocki, 214, 223.
ellenbergeri, 158, 223.
erythrocephala, 81, 223.
euphorbiae, Hemaspidoproctus, 151, 223.
euphorbiae, Steatococcus, 208, 214, **218,** 223.
ewarti, 203, 223.
fabricii, 223.
farinosus, **86,** 223.
fasciculensis, 48, 52, 53, 223.
ferox, 135, 138, 223.
festiva, 223.
ficus, 223.
filiferus, 41, 42, 43, 44, 223.
flava, 208, 223.
floriger, 141, 142, 143, 144, 223.
formicarum, Icerya, 203, 208, 223.
formicarum, Margarodes, 73, 75, 77, **78,** 223.
fortis, 140, 223.
frischii, 223.
fulleri, 140, 141, 223.
furcatus, 223.
fuscipennis, 122, 129, 144, 223.
fuscus, 177, 223.
gallicus, 77, 78, 223.
genistae, 208, 223.
ghesquierei, 158, 223.
giganteus, 158, 224.
glaber, 158, 224.
gorodetskia, 55, 56, 57, 224.
gowdeyi, 158, 214, 224.
Greenacoccus, 163, 219.
greeni, 77, 224.
Greeniella, 163, 219.
Guerinia, 197, 219.
Gueriniella, 195, 196, **197,** 219.
guerinii, 224.
gymnocarpi, 126, 127, 128, 224.
haematoptera, 171, 172, 189, 224.
hamelii, 77, 224.

hellenica, 92, 93, 94.
hellenicus, 92, 224.
Hemaspidoproctus, 11, 122, 123, 124, **148,** 219.
hempeli, 105, 106, 107, 224.
hiemalis, **77,** 224.
hirculus, 224.
hirsutissimus, 77, **78,** 224.
hirticornis, 224.
hirtus, 128, 224.
Homoptera, 28.
howardi, 167, **169,** 224.
hyperici, 208, 224.
hyphaeniacus, 139, 140, 224.
Icerya, 6, 7, 10, 11, 17, 18, 21, 22, 26, 103, 104, 105, 123, 155, 183, 189, 195, 196, 197, 199, 200, **203,** 208, 211, 212, 213, 214, 216, 217, 219.
Iceryini, 120, 159, **195,** 196.
illigeri, 224.
immane, 224.
immanis, **86.**
indicus, Margarodes, 77, 224.
indicus, Monophlebidus, 132, 133, 134, 224.
insulans, 208, 224.
jacobsoni, 203, 208, 224.
japonicus, 44, 224.
koebelei, **208,** 224.
Kuwania, 16, 19, 53, 55, 62, **64,** 65, 67. 219.
Kuwaniinae, 63.
Kuwaniini, 62, **63.**
Labioproctus, 11, 122, 123, 124, 125, **145,** 148, 219.
larreae, rileyi, 208, **209,** 224, 226.
Leachia, 128, 129, 144, 219.
leachii, 169, **170,** 224.
levis, crawfordi, 177, 180, 181, 223, 224.
lichenoides, 169, 224.
littoralis, 208, **210,** 224.
Llaveia, 10, 20, 136, 181, 182, **183,** 189, 191, 192, 219.
Llaveiella, 182, **192,** 219.
Llaveiini, 119, 120, **179,** 182.
longisetosa, 208, 224.
Lophococcus, 138, 151, 155, 219.
luederwaldti, 208, 224.
luzonica, 169, **170,** 189, 224.
macrocarpae, 45, 224.
mangiferae, stebbingii, 163, **169, 170,** 224, 227.
Marchalina, 21, 91, **92,** 219.
Marchalinini, 88, **91.**
margarodes, 225.
Margarodes, 5, 7, 10, 12, 19, **21, 23, 26, 28,** 29, 40, 62, 66, 69, 71, **72,** 73, 77, 79, 80, 81, 219.
Margarodidae, 8, 9, **30,** 219, 222.
Margarodinae, 7, 23, 29, 33, 34, 35, 40, **61,** 62, 191.
Margarodini, 29, 62, 63, **71,** 72.
maskelli, Drosicha, 164, 165, 166, 169, 225.
maskelli, purchasi, Icerya, 208, **209,** 225, 226.
Matsucoccini, 36, 37, **48.**
Matsucoccus, 6, 7, 11, 13, 16, 21, 27, 36, **48,** 219.
matsumurae, 13, 48, 49, 50, 51, 52, 53, 225.
maxima, Icerya, 208, **210,** 225.
maximus, Aspidoproctus, 14, 152, 153, 155, 156, 157, 158, 225.
maynei, 208, 225.
mediterraneus, 77, 225.
meridionalis, 73, 74, 77, **78,** 225.
mexicanorum, 184, 185, 186, 188, **189,** 225.
mexicanus, Cryptokermes, 100, 101, 103, **104,** 225.
mexicanus, rosae, Steatococcus, 214, 217, **218,** 225, 226.
mimeuri, 158, 225.
mimosae, littoralis, 208, **210,** 224, 225.
Mimosicerya, 12, 15, 16, 96, 97, **104,** 219.
minima, 208, **209,** 225.
minor, 208, **210,** 225.
mirabilis, 151, 154, 155, 156, 157, 158, 225.
Monophlebidus, 21, 122, 123, 124, 125, **132,** 219.
Monophlebinae, 6, 7, 17, 18, 21, 22, 23, 26, 28, 29, 33, 34, 92, 115, **117,** 119, 173, 195.
Monophlebini, 119, 120, **121,** 129, 138.
Monophlebites, 5.
Monophleboides, 23, 121, 122, 124, **125,** 129, 219.
Monophlebulini, 119, 120, **173.**
Monophlebulus, 6, 20, 22, 26, 163, 173, **174,** 177, 189, 219.
Monophlebus, 5, 65, 92, 121, 122, 123, 127, 128, 129 140, **144,** 160, 163, 177, 189, 195, 219.
montserratensis, 208, **211,** 225.
morrilli, 214, 215, 216, **218,** 225.
napiformis, 44, 225.
nardi, seychellarum, 208, **209,** 225, 226.
natalensis, 203, 208, 225.
neavei, 158, 225.
Neogreenia, 65, 219.
Neomargarodes, 12, 15, 26, 72, 77, **78,** 82, 219.
Neosteingelia, 11, 21, 30, 62, 64, **67,** 219.
newsteadi, 77, 225.
Newsteadiella, 203, 219.
Nietnera, 122, 123, 124, **129,** 219.
niger, 77, 79, 81, **82,** 225.
nigroareolata, 208, 225.
niveus, 225.
Nodulicoccus, 173, 174, **177,** 220.
nudatus, 214, **218,** 225.
oaxacoensis, 184, 187, 188, **189,** 225.
octocaudata, stebbingii, 169, **170,** 225, 227.
okadae, 208, 225.
Orthezia, 8, 21.
Ortheziidae, 9, 15.
Orthezliinae, 7, 8.
Ortonia, 183, 189, 191, 220.
ovilla, 144, 225.
Palaeococcus, 18, **92,** 122, **123,** 125, **128,** 129, 144, 208, 214, 220.
palavanica, 169, **170,** 225.
pallidus, 225.
palmeri, 208, **209,** 225.
papillosus, 77, **78,** 225.
Paracoelostoma, 23, 96, **97,** 220.
Paragreenia, 220.
parieli, 77, 78, 225.
parvus, 158, 225.
pattersoni, sulfurea, 208, 225, 227.
paulista, 208, 225.
peringueyi, 77, 225.
Perissopneumon, 18, 37, 122, **123,** 124, 125, **132, 135,** 141, 220.
perrisii, 77, 78, 225.
pertinax, 151, 158, 225.
peruviana, 97, 98, 99, 100, 225.
Phenacoleachia, 8.
philippinensis, 169, 225.
phyllanthi, **162,** 225.
Physokermes, 8.
piceae, 8.
pilosa, Coelostomidia, **117,** 225.
pilosa, Icerya, 208, **209,** 225.
pilosior, crawfordi, 114, 176, 223, 225.
pimentae, primitiva, 203, 226.
pini, 53, 226.
pinicola, 167, **169,** 226.
platani, 57, 58, 59, 60, 226.
Platycoelostoma, 88, **89,** 220.
Platycoelostomini, **88.**
plucheae, townsendi, 214, **218,** 226, 227.
poleii, 145, 146, 147, 148, 226.
polonicus, 5, 73, 77, 78, 226.
Porphyrophora, 5, 73, 220.
primitiva, 189, 190, 191, 192, 226.
Proticerya, 203, 220.
Protortonia, 17, 23, 182, **189,** 220.
Pseudaspidoproctus, 11, 121, 122, 124, 125, **138,** 220.
Pseudococcinae, 8.
Pseudococcus, 57.
pulcher, 208, **210,** 226.
pundaluoya, 129, 130, 131, 226.
purchasi, 6, 7, 189, 207, 208, **209,** 226.
quadricaudatus, 169, **170,** 226.
quercus, Kuwania, 65, 66, 226.
quercus, Xylococculus, 45, 226.
raddoni, 226.
rileyi, Icerya, 203, 208, **209,** 226.
rileyi, Margarodes, 77, **78,** 226.
rosae, 200, 201, 202, 203, 226.
ruber, 77, 226.
rubiginosus, **86,** 226.
sacchari, 203, 226.
samaraius, 214, **218,** 226.
sanguinea, 172, 189, 226.
Sasakia, 64, 220.
saundersii, 169, 189, 226.
schoutedeni, 208, 226.
schrottkyi, 208, **211,** 226.
senex, 123, 141, 144, 148, 226.
serratulae, 197, 198, 199, 226.
serrei, 138, 226.
seychellarum, 203, 204, 205, 206, 208, **209,** 226.
similis, Icerya, **211,** 226.
similis, Margarodes, 77, **78,** 226.
sjostedti, 128, 227.

Sphaeraspis, 73, 220.
splendida, 208, 227.
Steatococcus, 11, 158, 196, 197, 203, 208, **214,** 220.
stebbingii, 163, 164, **169, 170,** 227.
Steingelia, 20, 21, 26, 30, 54, **55,** 220.
Steingeliinae, 23, 29, 33, 34, 35, **53.**
Steingeliini, 54.
Stigmacoccini, 36, **37.**
Stigmacoccus, 16, 19, **37,** 45, 135, 220.
Stomacoccus, 11, 19, 20, 21, 25, 26, 28, 30, 45, 54, 55, 56, **57,** 220.
suaedae, 128, 227.
subandina, 208, **210,** 227.
subterraneus, 227.
sulfurea, 208, **211,** 227.
tabayae, 227.
tabernicolus, 214, **218,** 227.
taenechina, 192, 193, 194, 227.
tamarinda, 161, 162, **163.**
tamarindus, 160, 227.
tangalla, 208, 227.
taunayi, 208, 227.
tectonae, 161, **162,** 227.
Tessarobelus, 220.
texana, 67, 68, 69, 70, 71, 227.
theobromae, 214, **218,** 227.
tonilensis, littoralis, 208, **210,** 224, 227.
townsendi, Steatococcus, 214, **218,** 227.
townsendi, Drosicha, 163, **169, 170,** 227.
trabuti, 79, 80, 81, **82,** 227.
tremae, 208, 227.
tricornis, mirabilis, 158, 225, 227.
trilobitum, 227.
trimeni, 77, **78,** 227.
uhleri, 181, 183, 189, 227.
Ultracoelostoma, 13, 15, 16, 23, 96, **108,** 220.
variegatus, 169, **170,** 227.
verrucosus, 158, 227.
vitis, 227.
vitium, 77, **78,** 227.
vuilleti, 158, 227.
wairoensis, **117,** 227.
Walkeriana, 10, 20, 21, 122, 123, 124, 125, 135, 140, **141,** 145, 146, 148, 151, 220.
Warajicoccus, 163, 220.
westwoodi, 82, **86,** 227.
xyliae, 227.
Xylococcinae, 19, 23, 29, 33, 34, **35.**
Xylococcini, 36, 37, **40.**
Xylococculus, 14, 40, **44,** 48, 220.
Xylococcus, 7, 13, 15, 16, 23, 35, 40, **41,** 44, 45, 47, 48, 76, 82, 220.
zealandica, Coelostomidia, 112, 113, 114, 115, 116, **117,** 227.
zealandica, Phenacoleachia, 8.
zeteki, 208, **211,** 227.
zeylanica, 64, 67.
zeylanicus, 65, 227.
zimmermanni, 141, 227.

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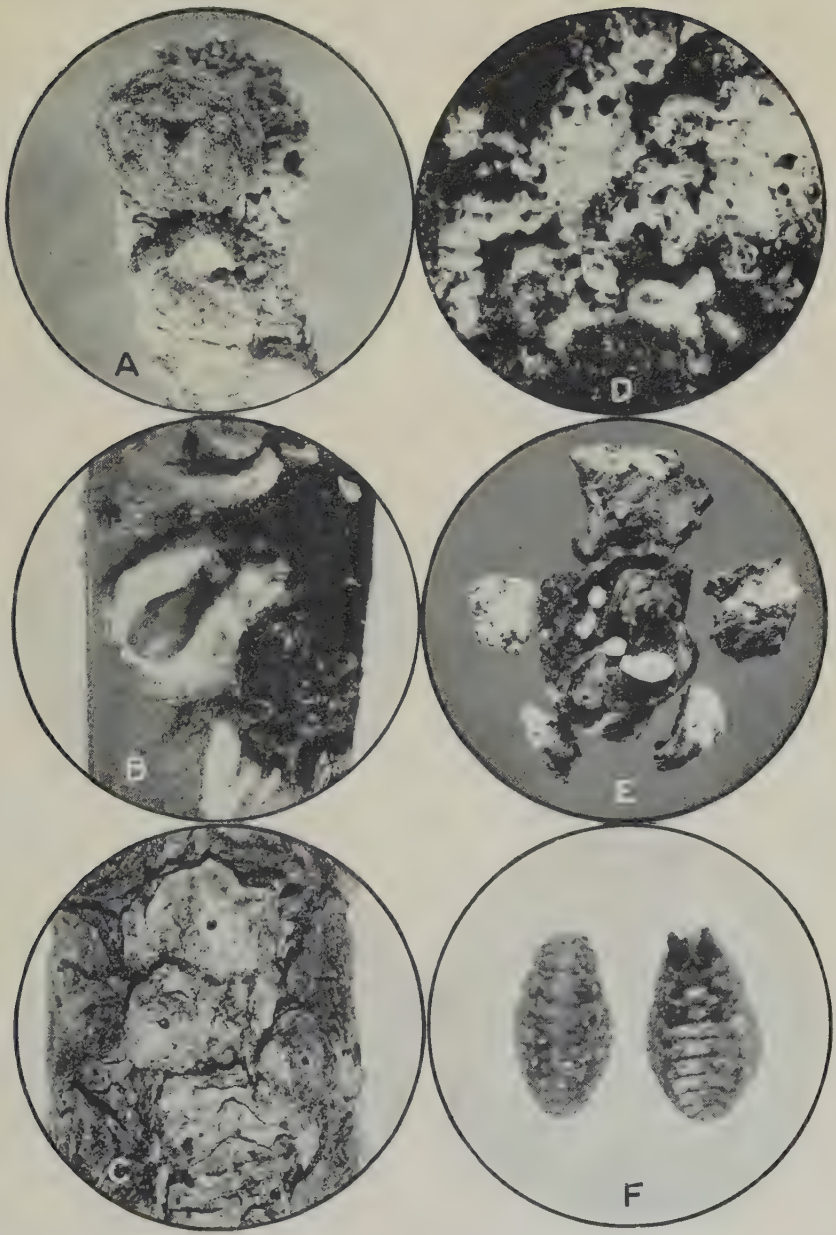
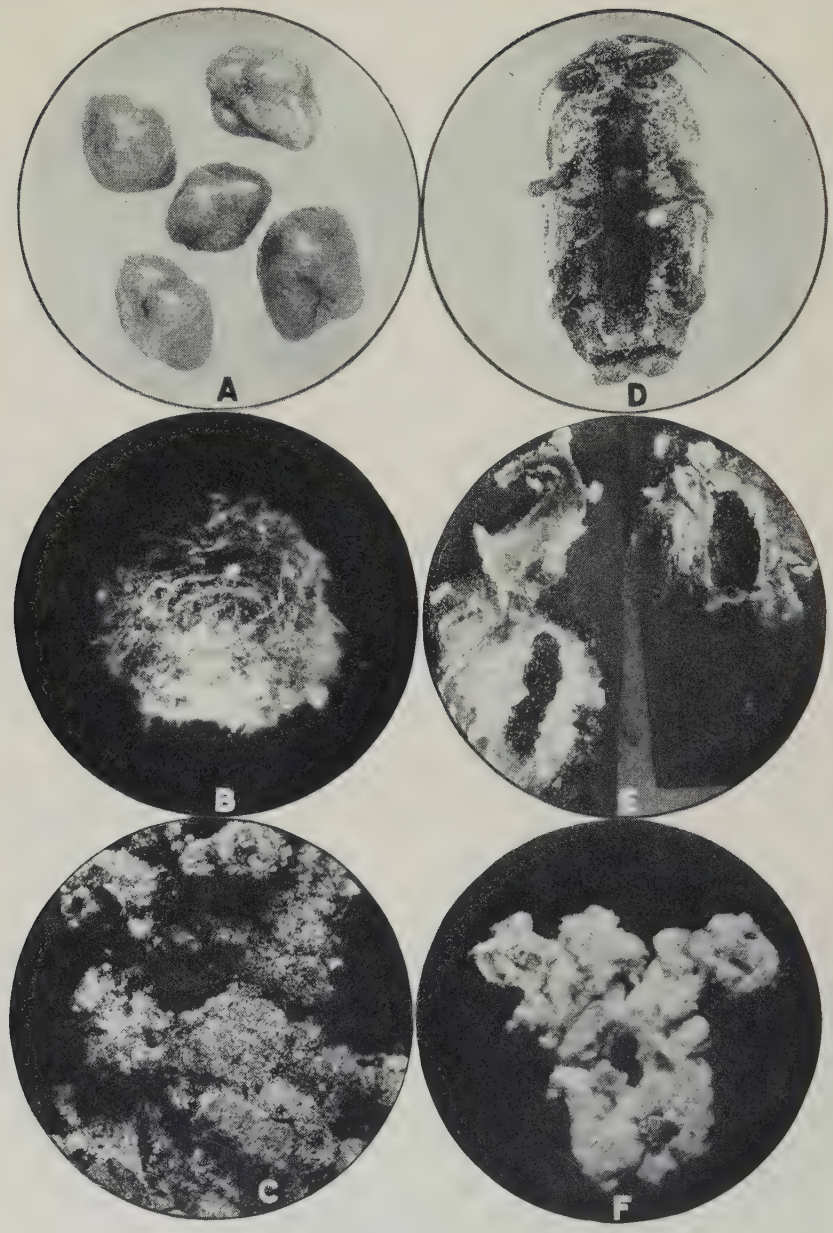


THE COCCID FAMILY MARGARODIDAE

A, *Stigmacoccus asper:* Test of preadult on bark. B, *Xylococculus betulae:* Immature female imbedded in white wax on piece of birch bark. C, *Matsucoccus matsumurae:* Twig of Pinus sp. showing swellings produced within bark, with tiny circular hole at apex of each swelling. D, *Kuwania quercus:* Mass of secreted material with insects imbedded in it on bark of Quercus sp. E, *Neosteingelia texana:* Bits of bark of Celtis sp. with white cottony secretion attached. F, *Margarodes formicarum:* Adult females, alcoholic specimens



THE COCCID FAMILY MARGARODIDAE

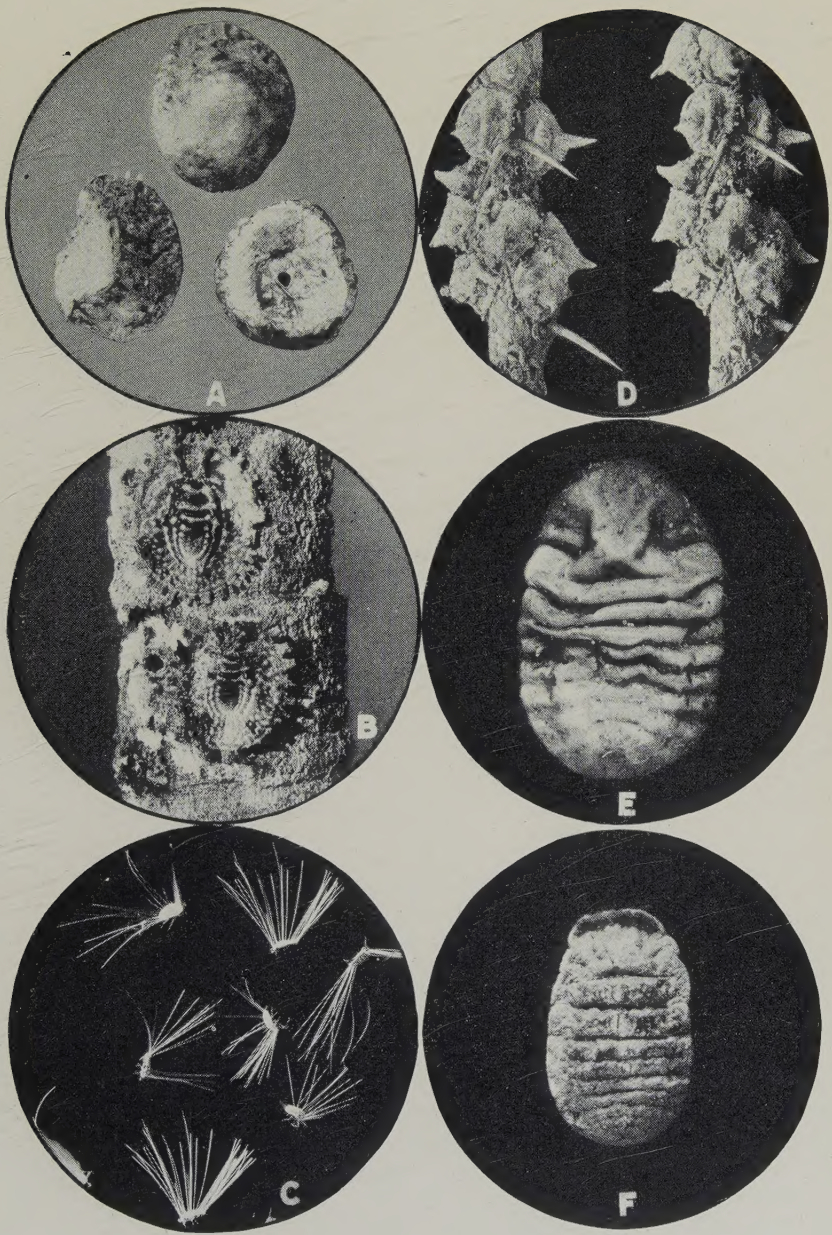
A, *Margarodes formicarum:* Tests of immature females, the so-called "ground pearls." B, *Neomargarodes trabuti:* Adult female, dried and shriveled specimen. C, *Neomargarodes trabuti:* Tests of immature females. D, *Callipappus australis:* Adult female, ventral aspect. E, *Platycoelostoma compressa:* Preadult females imbedded in white wax beneath bark of host. F, *Marchalina hellenicus:* Masses of white secretion produced by females

THE COCCID FAMILY MARGARODIDAE

A, *Paracoelostoma peruviana:* Tests produced during growth, two broken open. B, *Cryptokermes brasiliensis:* Tests of intermediate female on bark of host. C, *Mimosicerya hempeli:* Preadult female on bark of host. D, *Ultracoelostoma assimile:* Preadult tests and semigalls on twigs of host. E, *Coelostomidia zealandica:* Preadult tests on bark of host. F, *Monophleboides gymnocarpi:* Adult female, alcoholic specimen

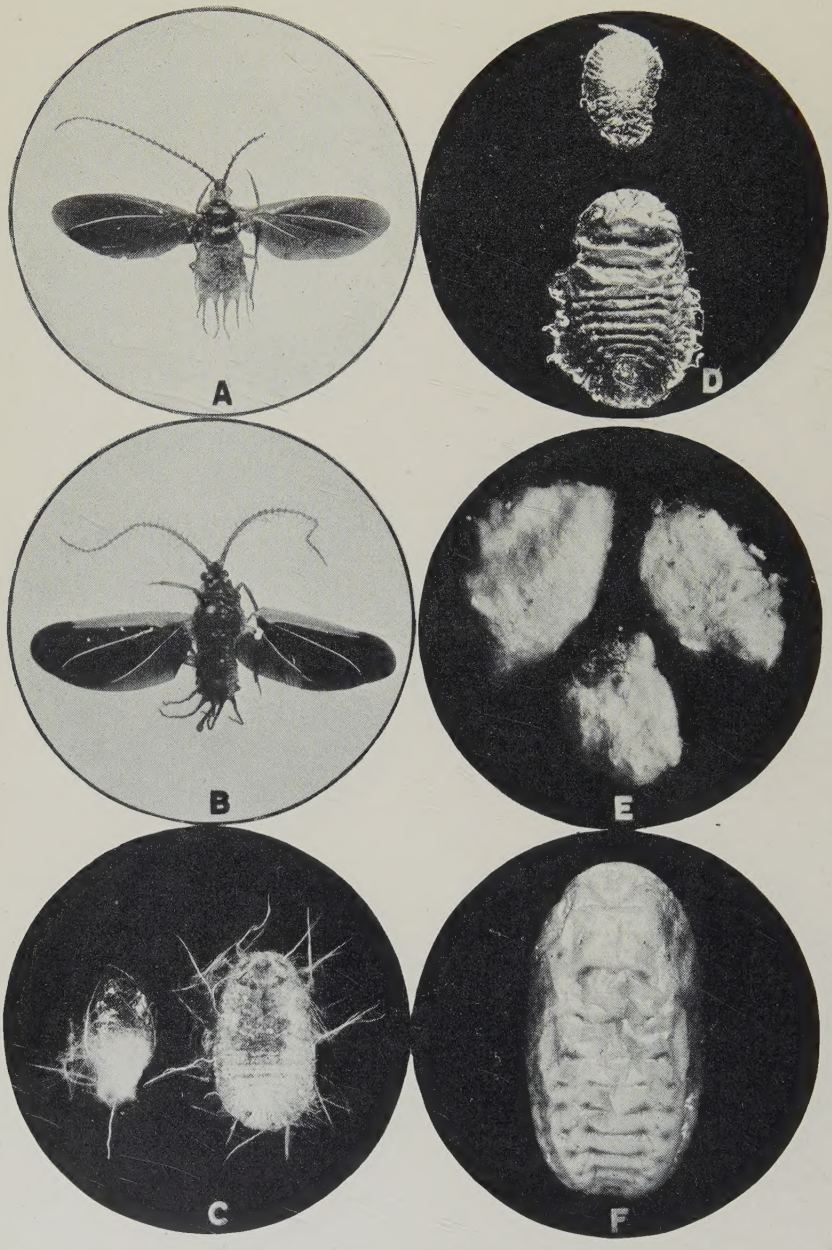
THE COCCID FAMILY MARGARODIDAE

A. *Monophlebidus indicus:* Adult female, dorsal aspect (broken). B, *Perissopneumon convexa:* Adult female, dorsal aspect. C, *Pseudaspidoproctus hyphaeniacus:* Adult female, dorsal aspect. D, *Walkeriana floriger:* Adult females, ventral and dorsal aspects. E, *Labioproctus poleii:* Adult female, dorsal aspect. F, *Hemaspidoproctus cinereus:* Adult female, dorsal aspect



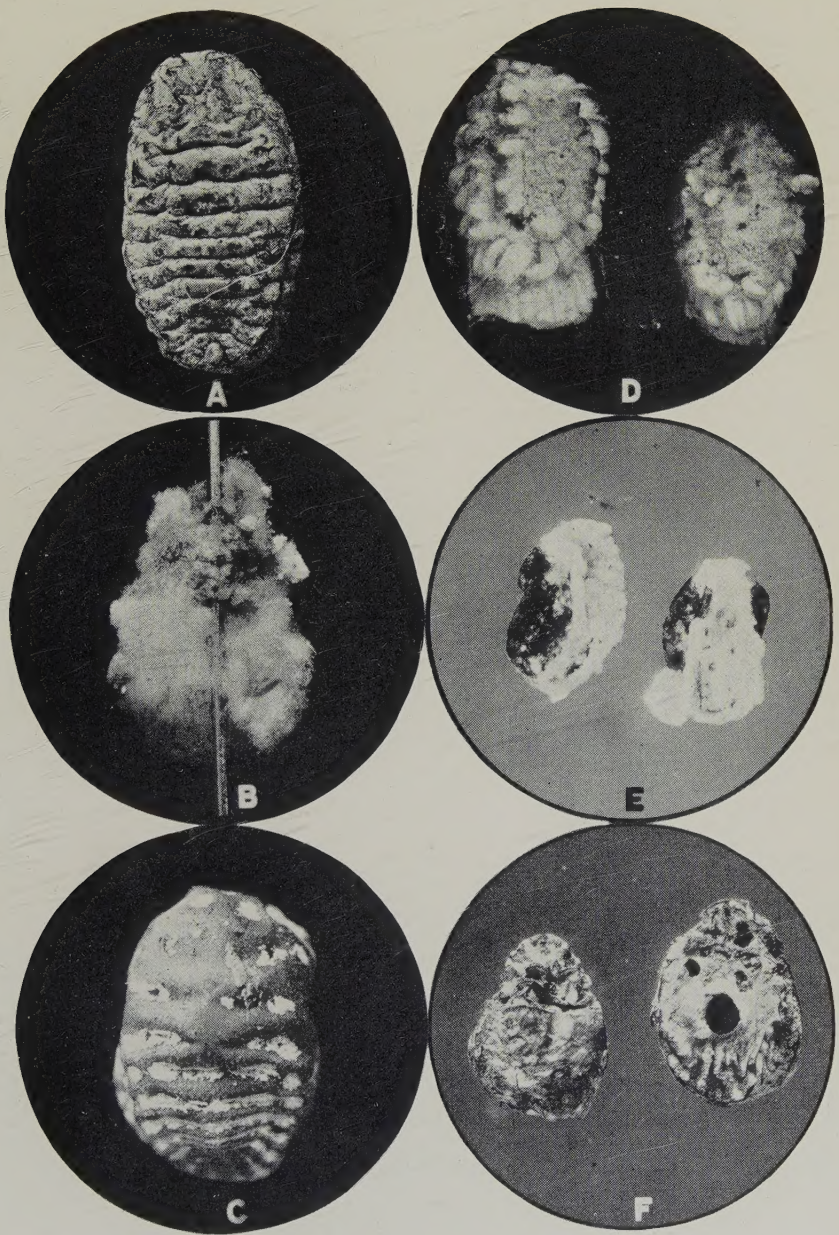
THE COCCID FAMILY MARGARODIDAE

A, *Aspidoproctus maximus:* Adult females, dorsal and ventral. (Photo by J. G. Sanders.) B, *Aspidoproctus maximus:* Early adult female before distension. (Photo by J. G. Sanders.) C, *Aspidoproctus maximus:* Larvae, showing long secretionary filaments. (Photo by J. G. Sanders.) D, *Aspidoproctus mirabilis:* Adult female, showing middorsal horn. (Photo by J. G. Sanders.) E, *Drosichiella tamarinda:* Adult female, denuded of secretion. F. *drosicha corpulenta:* Adult female, denuded of secretion



THE COCCID FAMILY MARGARODIDAE

A, Drosicha sp.: Adult male. B, *Drosichoides haematoptera:* Adult male. C, *Monophlebulus pilosior:* Adult females. D, *Nodulicoccus levis:* Adult females. E, *Llaveia oaxacoensis:* Adult females, shriveled and with ovisacs. F, *Llaveia oaxacoensis:* Adult female, dorsal from alcoholic specimen



THE COCCID FAMILY MARGARODIDAE

A, *Llaveiella taenechina:* Adult female, dorsal. B, *Gueriniella serratulae:* Adult female inclosed in mass of cottony secretion. C, *Crypticerya ?rosae:* Adult female, dorsal. D, *Icerya seychellarum:* Adult females, dorsal. E, *Auloicerya australis:* Adult females. F, *Steatococcus morrilli:* Adult females, dorsal and ventral